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Fishery Bulletin

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DISTRIBUTION OF MACROSCOPIC REMAINS OF RECENT ANIMALS FROM MARINE SEDIMENTS OFF MASSACHUSETTS

ROLAND L. WIGLEY[1] AND FREDERICK CHARLES STINTON[2]

ABSTRACT

Macroscopic animal remains are common constituents of bottom sediments on the continental shelf and upper continental slope south of Cape Cod, Mass. The largest quantities are in sandy deposits in the vicinity of Nantucket Shoals, where they form nearly 30% by volume of the total substrate. The smallest quantities are along the outer continental shelf and upper slope, where animal remains generally make up less than 1% of the substrate. Representatives of all three major realms of aquatic animals contribute to the prefossil skeleton assemblages; benthic forms are the principal components, nektonic forms are common, and planktonic forms are rare. The quantitatively dominant taxonomic groups present in the sediments are: echinoderms, mollusks, and teleosts.

Typical specimens of all groups represented in the samples are illustrated. Charts and graphs show the geographic and bathymetric distributions of the common species.

Durable remains of recently (up to several thousand years) deceased animals and plants constitute an important, but frequently overlooked, link between living organisms and their fossils. Reconstruction of the marine environment that existed in past geological ages can be better approximated when present-day marine populations and processes are well understood. A conventional approach used in paleobiological investigations is to equate the habits, ecological requirements, and functional morphology of fossil species with their living relatives (Ladd, 1957; and others). Consequently, a thorough knowledge of existing life is valuable to geological advancement. Events during the transitional phase between death and fossilization may strongly influence the dispersal, shape, and associated species of fossil remains. Frequently these events must be clearly understood to interpret fossil findings correctly and completely. It is in this context that the prefossil stage is considered to be significant in determining the history of life.

A series of samples collected from the ocean bottom off southeastern Massachusetts provide an insight into the composition and the geographic distribution of macrobenthic, nektonic, and planktonic animal skeletons—or portions thereof—that occur in continental shelf bottom sediments and that are available for fossilization. Thus the purpose of this report is to describe qualitatively and quantitatively the macroscopic animal remains (durable portions of recently dead animals) in the bottom sediments of this representative portion of the continental shelf in New England.

To avoid undue repetition of the words "dead," "deceased," "remains," and similar descriptive terms throughout this report, it must be emphasized at the outset that all samples of animal materials dealt with in this report are the remains of dead animals. Accounts of the living organisms obtained in these collections will be dealt with in other reports.

Previous studies of paleontological interest pertaining to prefossil marine animal remains are very diverse in subject. A few examples of these studies include such dissimilar topics as: the composition and distribution of mollusk shell remains (Habe, 1956; and others), biological alteration of bottom sediments (Schäfer, 1956; Rhoads, 1966; and others), comparison

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of the feeding habits and sediment types inhabited by epifaunal and infaunal benthic animals (Craig and Jones, 1966), catastrophism in the sea (Gunter, 1947; and others), position of pelecypod shells in different environments (Emery, 1968), burial of mollusk shells (Johnson, 1957), radiocarbon dating of relict oyster shells (Merrill, Emery, and Rubin, 1965), and other related subjects. Most of these studies are restricted to one specific topic. The present study, likewise, has a limited objective: to describe the species composition and distribution of macroscopic prefossil animal remains.

Literature pertaining to present-day mollusk remains in marine bottom deposits is relatively common; see references in Habe (1956), Schäfer (1956), Johnson (1957), Belyaev (1970), and others. In contrast, however, a paucity of reports dealing with prefossil fish remains became strikingly evident during our literature search. Research on this subject tends to be regionally oriented. For example, the study by Jensen (1905) deals with otoliths from an Arctic basin. David (1947) and Soutar (1967) described fish remains from off southern California, and Belyaev and Glikman (1970) describe selachian teeth from a broad expanse of the Pacific Ocean. A major exception to this regional basis is the report by Brongersma-Sanders (1949), which summarizes the earlier literature pertaining to fish remains (albeit mostly fossil) from many parts of the world.

Prefossil remains of marine organisms are more easily obtained than are those of most terrestrial or aerial forms. Macrobenthic and nektonic organisms are usually abundant on continental and insular shelves, and their skeletal components are massive compared with those of microplanktonic pelagic forms. As a result, the "fossil assemblages" (Craig, 1953) of the continental shelf are dominated by macroscopic organisms, as opposed to planktonic forms that make up the bulk of deep-sea fossils. Likewise, the prefossil material of organic origin on continental and insular shelves is generally of a larger size, and the macrofaunal components are considerably more abundant than they are in the deep sea.

MATERIALS AND METHODS

Samples were collected 11-20 June 1962, from the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) RV *Delaware* at 62 stations south of Martha's Vineyard, Mass. (Table 1; Figure 1). Stations were spaced at intervals of 16 km on a grid pattern having eight north-south transects at right angles to the depth contours. Quantitative bottom samples, including sediments and the constituent benthic fauna, were collected with a Smith-McIntyre grab sampler (Smith and McIntyre, 1954). This instrument effectively sampled a 0.1-m² area of bottom to a depth of about 10 to 17 cm. The volume of bottom material analyzed from individual samples averaged 8.9 liters. At sea, contents from the grab were washed on a 1-mm mesh sieving screen. Material remaining on the screen after washing was removed and preserved in a solution of neutral Formalin.[3] In the laboratory ashore.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

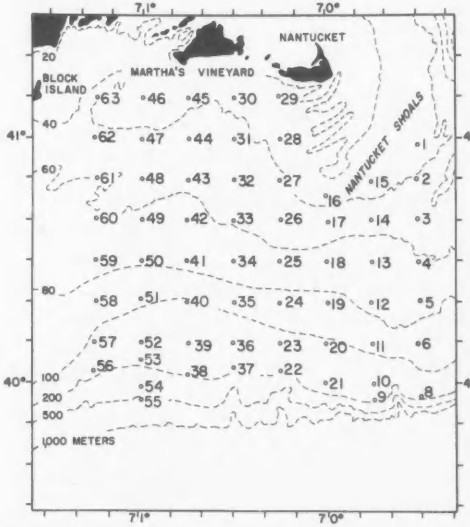

FIGURE 1.—Location of stations at which bottom samples were collected for determining the distribution of the remains of marine animals. Isobaths are indicated by dashed lines.

TABLE 1.—Station location, water depth, sediment type, and volume of bottom samples collected south of Martha's Vineyard, Mass., 11-20 June 1962.

Station number	Lat N	Long W	Water depth	Sediment type	Sample volume
			m		liters
1	40°58′	69°30′	46	Sand & gravel	2
2	40°51′	69°31′	46	Sand	4½
3	40°40′	69°31′	51	Sand	2¾
4	40°30′	69°29′	62	Sand	6¾
5	40°21′	69°30′	76	Sand	3¾
6	40°10′	69°31′	91	Sand	5¾
8	39°57′	69°30′	183	Sand	4¾
9	39°56′	69°45′	201	Sand	3¾
10	40°00′	69°45′	139	Silty sand	4¼
11	40°10′	69°45′	95	Silty sand	4¼
12	40°20′	69°46′	79	Sand	6¼
13	40°30′	69°45′	73	Sand	9¾
14	40°40′	69°45′	59	Sand	4½
15	40°50′	69°45′	37	Sand	6
16	40°46′	70°00′	38	Sand	2¾
17	40°39′	69°59′	49	Sand	4¾
18	40°30′	70°00′	73	Sand	11¾
19	40°20′	69°59′	91	Sand	7
20	40°10′	70°00′	117	Sand	¾
21	40°00′	70°00′	165	Sand	10¼
22	40°03′	70°15′	183	Silty sand	9¾
23	40°10′	70°15′	113	Silty sand	12¾
24	40°20′	70°15′	90	Silty sand	14¾
25	40°30′	70°15′	70	Sand	14
26	40°40′	70°15′	51	Sand	10
27	40°50′	70°15′	44	Sand	9¼
28	41°00′	70°15′	33	Sand	7¾
29	41°11′	70°16′	27	Sand	4¾
30	41°10′	70°30′	38	Sand	10
31	41°00′	70°30′	48	Sand	9¾
32	40°50′	70°30′	59	Sand	14¼
33	40°40′	70°30′	62	Silty sand	14¾
34	40°30′	70°30′	73	Sandy silt	13¾
35	40°20′	70°30′	97	Sandy silt	10¾
36	40°10′	70°30′	128	Silty sand	14¾
37	40°04′	70°29′	220	Sand	11½
38	40°02′	70°44′	194	Silty sand	5¾
39	40°10′	70°45′	132	Silty sand	14¾
40	40°20′	70°46′	106	Sand-silt-clay	14¾
41	40°30′	70°45′	79	Sandy silt	14¼
42	40°40′	70°45′	66	Silty sand	7½
43	40°50′	70°45′	55	Sand	9¾
44	41°00′	70°45′	51	Sand	7¾
45	41°10′	70°45′	38	Sand and gravel	5
46	41°10′	71°00′	40	Sand	6½
47	41°00′	71°00′	51	Sand and gravel	12¼
48	40°50′	71°00′	59	Sand	4¾
49	40°40′	71°00′	70	Sandy silt	14¾
50	40°30′	71°00′	84	Clayey silt	14
51	40°21′	71°00′	99	Sandy silt	14¾
52	40°10′	71°00′	146	Silty sand	4¾
53	40°06′	71°00′	179	Silty sand	11¾
54	39°59′	71°00′	366	Silt	11¾
55	39°56′	71°00′	567	Silt	10
56	40°03′	71°16′	183	Sand	10¾
57	40°10′	71°15′	110	Silty sand	7¾
58	40°20′	71°15′	91	Silty sand	14½
59	40°30′	71°15′	77	Silty sand	14¼
60	40°40′	71°15′	62	Sand	14½
61	40°50′	71°15′	62	Sand	12¾
62	41°01′	71°16′	48	Sand	¾
63	41°10′	71°15′	38	Sand	4¾

mineral matter and associated debris were removed by hand sorting, and the animals and animal remains were separated by species, identified, and counted. Only animal remains are considered in the present report.

Water depths at which samples were collected ranged from 27 to 567 m.

Sediment samples were collected at each station and at two localities equally spaced between stations along the cruise track. Of the 186 samples collected, 60 were analyzed in detail for particle size, and the remaining 126 were examined in the laboratory by field techniques. Names of the various sediment types are in accordance with the classification reported by Shepard (1954) and Emery (1960).

DESCRIPTION OF THE AREA

Three major physical features that have an important impact on the occurrence, distribution, and condition of the prefossil animal remains in this area are: physiography, bottom sediment composition, and hydrography. These features are briefly discussed below.

PHYSIOGRAPHY

The area studied is about 130 km square and extends across the continental shelf and the upper portion of the continental slope. Bottom configuration is moderately smooth; water depths increase gradually and rather uniformly from shore outward to the shelf break, which is at a depth of about 120 m. Beyond the shelf break, on the continental slope, the depth gradient is relatively steep, averaging 4°. Detailed bathymetric charts of this area having contour intervals of 1 fathom were published in 1967 by the U.S. Department of Commerce and U.S. Department of the Interior (Coast and Geodetic Survey, Bathymetric Maps numbers: 0708N-52 and 53; 0808N-51 and 52; and 0807N-51).

BOTTOM SEDIMENT COMPOSITION

Bottom sediments in the area are composed of relict glacial material—principally nonbiogenic sands and silts plus a few gravel patches

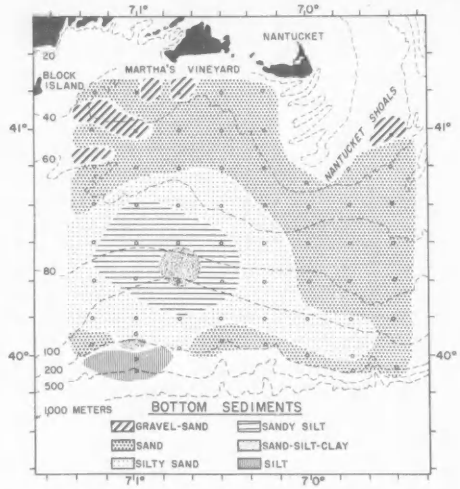

FIGURE 2.—Distribution of the various types of bottom sediments in the study area. Terminology is based on the classification reported by Shepard (1954) and Emery (1960).

of glacial erratics. Six major sediment types occur in the area (Figure 2). The terminology used is based on the standard Wentworth particle size classification (Twenhofel and Tyler, 1941; and others) and the nomenclature is that of Shepard (1954) and Emery (1960). Three types—sand, silty sand, and sandy silt—are distributed over a rather large area; the other three—gravel-sand, sand-silt-clay, and silt—have limited areal distributions. Sands cover more than half of the area. They occur mainly in shallow water (less than 60 to 80 m), except in the eastern sector and in a narrow (6 km) band parallel to the isobaths just below the outer periphery of the continental shelf. Sands and silts in the vicinity of the shelf break are primarily glauconitic. In shallow waters near Nantucket and Martha's Vineyard and in the vicinity of Nantucket Shoals, the sands are silt free and occasionally mixed with large quantities of shell. Mixtures of sand and gravel also occur in scattered patches in the shallower waters of the northwest sector and in Nantucket Shoals. Limonitic pellets and sand particles heavily stained with iron oxide are common in the northwest sector. Admixtures of silt occur with the sand over most of the remaining area.

A large (80 by 100 km) area of fine-grained sediments is situated in the southwestern sector. A relatively small circular area of sand-silt-clay near its center is surrounded by an inner band of sandy silt and an outer band of silty sand. Characteristically, the relatively large sand grains throughout the area of fine-textured sediments are frosted rounded quartz particles. Pyrite-filled foraminiferal tests occur in the eastern portion.

On the continental slope below the sand zone, the dominant sediment component is silt.

Additional information concerning sediments of this area and references to the geological literature were given by Uchupi (1963), Wigley and McIntyre (1964), Emery, Merrill, and Trumbull (1965), Emery (1966), Garrison and McMaster (1966), McMaster and Garrison (1966), and Wigley and Emery (1967).

HYDROGRAPHY

Within the area the water temperature regime is typically warm-temperate, although the boreal influence is seasonally significant. Surface temperatures are substantially higher than bottom temperatures; offshore surface waters are somewhat warmer than inshore waters throughout most of the year; temperatures of the entire water column change seasonally and to some extent from year to year. Most pertinent to the subject of this report are bottom water temperatures and nontidal currents.

A cell of cold (6.6°C in June 1962) bottom water extends in an east-west band from the New York region eastward to long 70°W (eastern Nantucket Island). This cell occurs at depths of about 40 to 80 m, which is roughly the midshelf region. At 300 to 600 m the bottom water temperatures are low and nearly constant throughout the year; they generally range between 4° and 7°C. Near the shelf break and upper continental slope the bottom temperatures are substantially higher, but also nearly constant; values range near 10° to 12°C throughout the year. Offshore shelf waters, especially in shallow sectors, may range from 3°C in Feb-

ruary-March to 14°C in September-November. Temperatures of inshore surface waters substantially exceed these values.

Nontidal movements of water masses on the continental shelf within the area are generally westward. Water in the Gulf of Maine and Nantucket Sound tends to flow southwesterly across Nantucket Shoals and into the area. Conversely, surface waters offshore beyond the continental shelf flow easterly. Authors who have published further information on the hydrography of the area include Bigelow (1927, 1933), Bumpus and Day (1957), Bumpus et al (1957), Day (1958), and Colton (1964, 1968, 1969).

ORDER OF DISCUSSION

The most common animal remains in the samples studied were echinoderms, mollusks, and fish. Considerably less common than the foregoing were remains of crustaceans and coelenterates. The order in which these groups are discussed below is according to the abundance of remains in each major group, namely, echinoderms, mollusks, fish, and crustaceans and coelenterates.

REMAINS OF ECHINODERMS

Echinoderms were the most numerous and quantitatively dominant group of animal remains occurring in the area. The sole contributors in this group were the echinoids. Spines and test fragments were rare to very abundant and were widely distributed. Presumably the skeletal fragments of asteroids and ophiuroids, of which living members of both groups are common in this region, were generally too small to be recovered using the 1-mm mesh screen. Of all macroscopic animals in the samples, the common sand dollar, *Echinarachnius parma* (discussed in the following subsection), was by far the leading component. Spines were the principal structures recovered from heart urchins and sea urchins. Some examples of typical echinoderm remains are illustrated in Figure 3.

The size of fragments of most organisms discussed in this section ranged from 1 mm (sand size) to 1 cm or more. The largest remains were tests of whole or nearly whole *E. parma*. Adult size of living members of this species (about 7 cm) is less than some of the other nonmolluskan species, but the comparatively strong, compact test is much more resistant to fracture. This durability, plus the enormous supply in the form of living individuals, contributed to the abundance of fragments of this species in the sediments. Counting the *E. parma* and other echinoids was impractical owing to the enormous numbers of small fragments, plus a gradation in size that precluded the separation of major fractions from minor ones. Occurrence of *Brisaster fragilis*, *Echinarachnius parma*, and *Strongylocentrotus drobachiensis* are listed by stations in Table 2.

ECHINARACHNIUS PARMA

Remains of *E. parma* were widespread (Table 2) and numerous. This species ranked first in volume and number of fragments of all organic remains in the study area; it occurred at 73% of the stations. It was most abundant in the vicinity of Nantucket Shoals (stations 2, 3, and 16). *E. parma* fragments made up nearly 30% (by volume) of the substrate near station 3. In deepwater areas in the vicinity of the middle and outer shelf, the density of fragments was low—occasionally less than 50/m² or about 0.01% by volume. (All animal remains combined generally formed less than 1% by volume of the substrates of the outer shelf and slope.)

The distribution of *E. parma* extended from the shallow inshore areas across the entire shelf to the upper portion of the continental slope (Figure 4). Surprisingly, it was rather sparse near the middle of the shelf. Fragments from inshore areas were different in size, color, and sphericity from those collected offshore. Test fragments from the inshore zone, which extends out to 50 or 70 m, were whitish, usually larger than 5 mm in greatest dimension, and had sharp and angular edges and apexes (Figure 3A). Fragments from depths of about 80 m or more were greenish-brown, commonly less than 5 mm long, and had rounded edges. In contrast to the fresh, new appearance of the test fragments

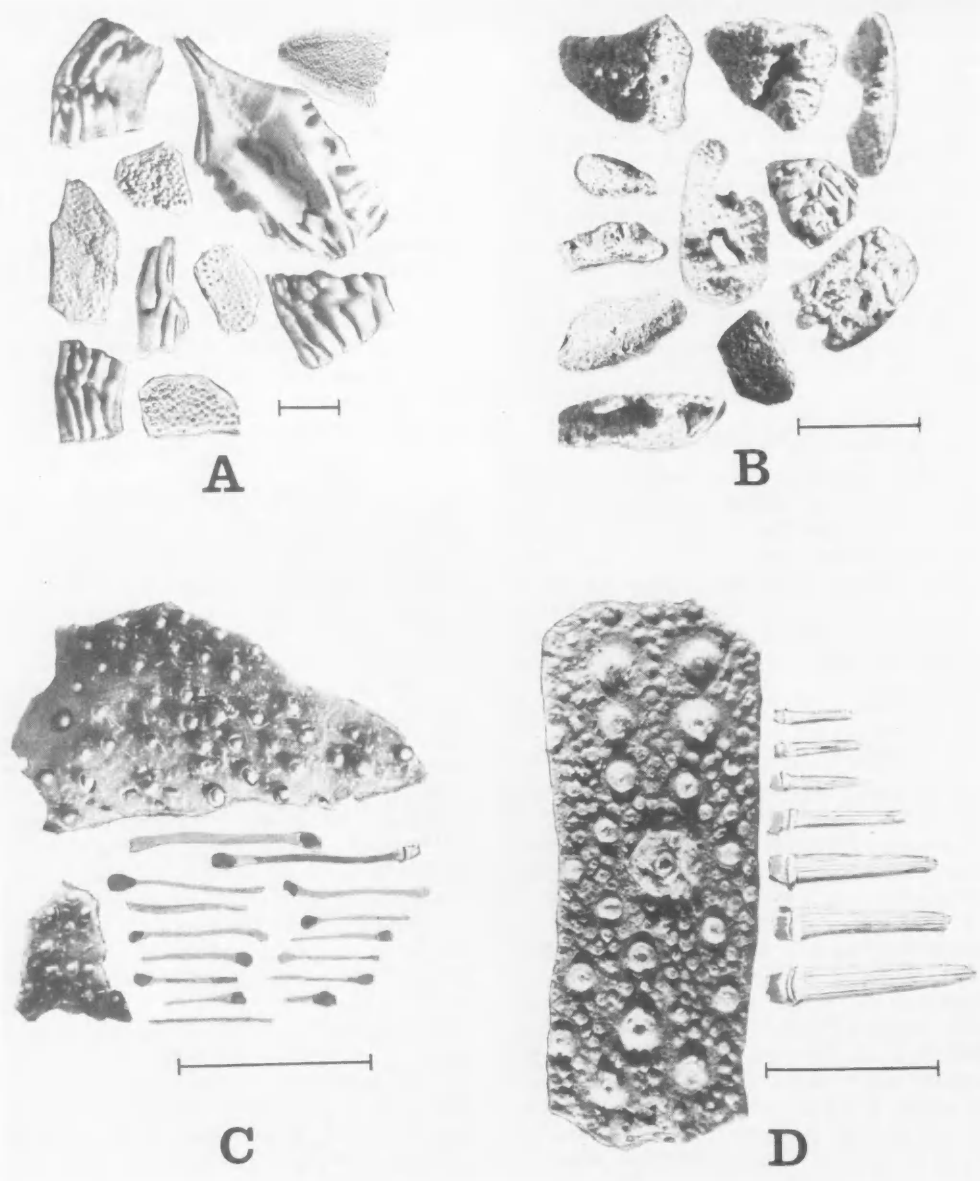

FIGURE 3.—Skeletal remains of echinoderms. A - *Echinarachnius parma*, test remains from shallow water; B - *E. parma*, test remains from deep water; C - *Brisaster fragilis*, test fragments and spines; D - *Strongylocentrotus drobachiensis*, test fragments and spines. Each scale bar is 5 mm.

TABLE 2.—Occurrence, by station, of the remains of three species of echinoderms. Present (+), absent (—).

Station number	*Echinarachnius parma*	*Brisaster fragilis*[1]	*Strongylocentrotus drobachensis*
1	+	—	+
2	+	—	—
3	+	—	—
4	+	—	—
5	+	—	—
6	+	—	—
8	—	+	—
9	+	—	+
10	+	—	—
11	+	+	—
13	+	—	—
14	+	—	—
15	+	—	—
16	+	—	+
17	+	—	—
18	+	—	—
20	—	+	—
21	+	+	—
22	+	+	—
23	+	+	—
24	+	+	—
26	+	—	—
27	+	—	—
28	+	—	—
29	+	—	—
30	+	—	—
31	+	—	—
33	+	—	—
35	+	+	—
36	+	+	—
37	—	+	—
38	+	+	+
39	—	+	—
40	+	+	—
41	+	—	—
43	+	—	—
44	+	—	—
45	+	—	—
46	+	—	—
47	+	—	—
49	+	—	—
51	+	+	+
52	+	+	+
53	+	+	—
54	—	+	—
56	+	+	—
57	+	—	—
61	+	—	—
62	+	—	—
63	+	—	—

[1] May include some fragments of *Echinocardium* or *Schizaster*.

from the inshore zone, shells from deep water appeared old and worn (Figure 3B). The characteristics of specimens from the area between the two depth zones were intermediate.

OTHER SPECIES

Brisaster fragilis (Figure 3C) was distributed in a broad east-west band along the outer

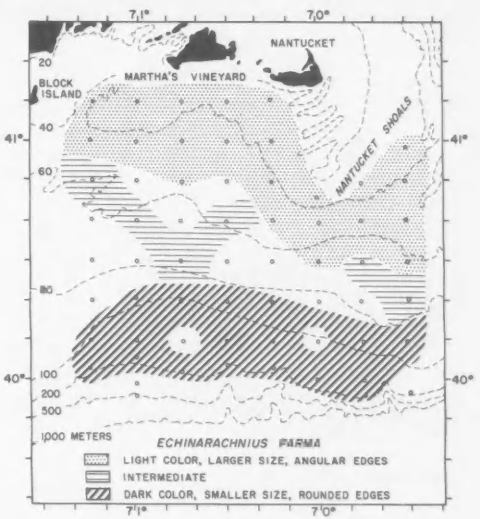

FIGURE 4.—Geographic distribution of remains of tests of *Echinarachnius parma*. Three categories of size, color, and sphericity are shown separately.

continental shelf and upper slope (Figure 5). The fragments were generally small and scattered. Even when all species are considered as a group, only a few spines or test fragments occurred in any one sample. Range in water depth for this echinoid was 90 to 366 m. Water depth range is compared with that of other species of echinoderms in Table 3 and illustrated in Figure 6.

The green sea urchin, *Strongylocentrotus drobachiensis* (Figure 3D), was represented chiefly by spines and less commonly by test fragments. The remains were rather widely scattered among six stations; two were in the

TABLE 3.—Bathymetric distribution of three species of echinoderms and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Brisaster fragilis[1]	90	366	155	18
Echinarachnius parma	27	201	84	45
Strongylocentrotus drobachiensis	38	201	121	6

[1] May include some spines of *Echinocardium* and *Schizaster*.

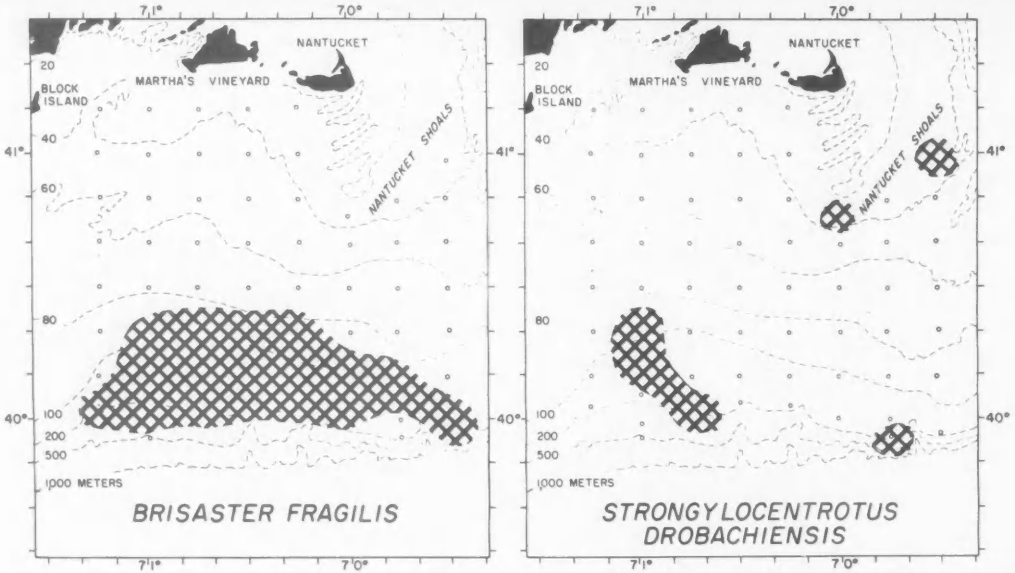

FIGURE 5.—Geographic distribution of skeletal remains of the echinoderms *Brisaster fragilis and Strongylocentrotus drobachiensis.*

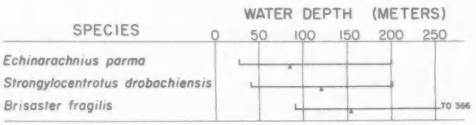

FIGURE 6.—Bathymetric range and mean depth of occurrence of echinoderm remains. (Mean values are listed in Table 3.)

shallow waters of Nantucket Shoals and the other four were in moderate to deep water near the shelf break (Figure 5). Bathymetric range at the locations where this species was found was from 38 to 201 m (Table 3, Figure 6).

REMAINS OF MOLLUSKS

Remains of mollusks were among the most common organic seabed constituents. In total abundance they ranked second; only the echinoderms were more plentiful. Four major groups of mollusks were represented in the material analyzed. Pelecypods were the most abundant molluscan group, gastropods ranked second, and the cephalopods and scaphopods were present in relatively small quantities. These groups are discussed below in the order of their abundance.

PELECYPODS

Pelecypod shells were abundant and conspicuous components of the prefossil animal remains. In addition to their relatively large size, often the color and texture of the shell surface contrasted sharply with the sediments in which they occurred. Size of the shells ranged from such large, robust species as *Spisula solidissima* (12 cm), *Arctica islandica* (10 cm), and *Placopecten magellanicus* (10 cm), to such small, fragile forms as *Thyasira gouldi, Nucula proxima, Bathyarca pectunculoides,* and others, all of which were 5 mm or less. A total of 57 species representing 40 genera were collected. Typical species are illustrated in Figure 7. Pelecypod remains were very widespread; they were collected at all stations except three (3, 47, and 62).

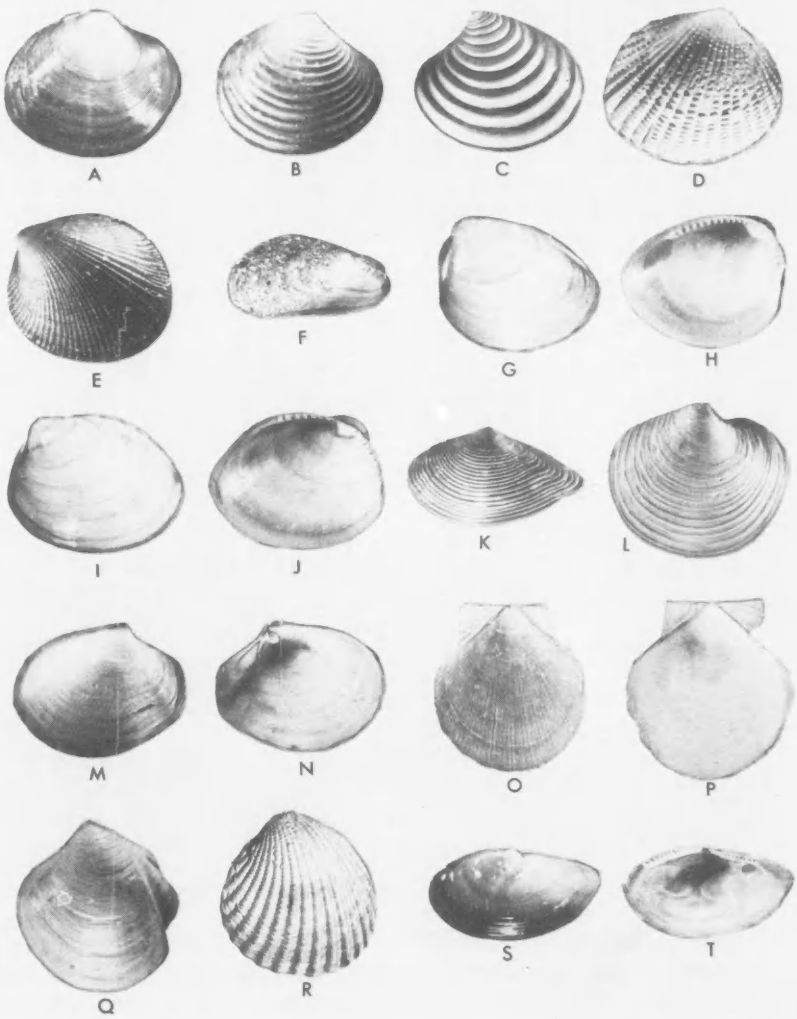

FIGURE 7.—Representative pelecypods from off southeastern Massachusetts. A - *Arctica islandica* (×0.7); B - *Astarte subequilatera* (×1); C - *Astarte undata* (×2); D - *Cerastoderma pinnulatum* (×2.6); E - *Crenella glandula* (×4); F - *Modiolus modiolus* (×0.7); G - *Nucula proxima* (×5); H - *Nucula proxima*, interior (×5); I - *Nucula tenuis* (×3.3); J - *Nucula tenuis*, interior (×3.3); K - *Nuculana acuta* (×4); L - *Phacoides filosus* (×2.6); M - *Periploma papyracea* (×2.6); N - *Periploma papyracea*, interior (×2.6); O - *Placopecten magellanicus*, left valve (×0.7); P - *Placopecten magellanicus*, right valve (×1); Q - *Thyasira trisinuata* (×3.3); R - *Venericardia borealis* (×1.3); S - *Yoldia sapotilla* (×2); T - *Yoldia sapotilla*, interior (×2).

Table 4.--Species and density (number per square meter), by station, of the common pelecypods.

Station number	Anomia aculeata	Arctica islandica	Astarte castanea	Astarte subaequilatera	Astarte undata	Bathyarca pectunculoides	Cetastoderma pinnulatum	Cremella decussata	Cremella glandula	Cuspidaria perrostrata	Cyclopecten thalassinus	Ennucula tenuis	Limatula subauriculata	Limopsis sulcata	Lyonsia hyalina	Mesodesma arctatum	Modiolus modiolus	Musculus niger	Nucula cebuana	Nucula tenuis	Nuculana acuta	Pandora gouldiana	Periploma leanum	Periploma papyracea	Phaseoles blakeanus	Phaseoles filosus	Pitar northumi	Placopecten magellanicus	Spisula solidissima	Thyasira gouldi	Thyasira ovata	Thyasira plana	Thyasira trisinuata	Venericardia borealis	Yoldia sapotilla	Unidentified
1	20	-	150	-	-	-	-	-	10	-	-	-	-	-	-	-	30	-	-	-	*	-	*	*	*	*	*	-	*	*	*	-	*	-	-	10
2	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30
4	-	10	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	80	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	40	10	-	60	
6	30	160	10	1,560	-	-	-	110	-	10	-	-	-	-	-	30	-	-	-	10	-	10	-	30	-	90	-	30	30	-	-	-	150	2,120	160	60
8	30	-	-	30	10	70	110	-	50	10	20	-	-	-	-	-	-	-	-	-	170	-	-	-	-	90	-	-	+	-	-	100	20	10	90	160
9	70	-	-	-	110	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	-	-
10	10	-	-	100	660	20	-	-	-	-	-	-	-	40	-	-	-	-	10	-	160	-	-	-	-	250	20	-	-	-	-	-	20	200	30	-
11	-	130	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40	-	170	-	150	-	-	-	-	110	70	80	10
12	-	40	-	-	40	-	120	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	30	-	-	-	-	140	20	20	30
13	-	40	-	-	130	-	60	30	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	10	-	-	-	-	110	-	30	-
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
16	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	-	-	-	-	-	10
17	-	10	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-
18	-	760	-	-	10	-	10	70	20	-	-	-	-	-	-	-	-	-	50	10	-	-	-	-	-	10	-	30	-	-	-	-	230	-	50	-
19	-	20	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	80	-	70	-	40	-	-	-	-	50	-	50	-
20	-	-	-	-	50	-	10	-	-	-	-	-	-	-	-	-	-	-	40	-	20	-	-	-	-	80	-	-	-	-	-	-	60	160	-	-
21	-	-	-	50	280	-	30	-	-	-	-	-	10	-	-	-	-	-	-	-	550	-	-	-	-	190	-	10	-	-	-	-	10	150	160	10
22	40	-	-	290	40	10	120	-	-	10	-	-	10	-	-	-	-	-	40	-	760	-	-	-	-	240	-	10	-	-	-	-	40	70	90	-
23	-	-	-	-	170	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	40	10	-	10	-	-	-	-	10	120	-	-
24	-	70	-	-	10	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	20	-	-	-	50	-	-	-	80	20	20	-
25	-	2,080	-	-	-	-	60	-	110	-	-	-	-	-	-	-	-	-	250	40	-	30	-	30	-	-	-	30	-	-	-	-	1,160	-	350	-
26	-	40	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	1,360	230	-	-	-	30	-	-	-	-	-	-	-	-	70	-	40	-
27	-	50	-	-	10	-	50	-	-	-	-	-	-	-	-	-	-	-	1,360	250	-	-	-	90	-	10	-	-	-	-	-	-	-	-	360	-
28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	10
29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-
30	-	-	-	-	20	-	20	-	-	-	-	-	-	-	-	-	-	-	90	-	-	-	-	-	-	-	20	-	-	-	-	-	120	30	10
31	-	-	-	-	30	-	30	-	-	-	-	-	-	-	-	-	-	-	60	-	-	-	20	20	-	20	20	-	-	-	-	10	-	50	-
32	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	140	-	-	-	-	-	130	-	90	-
33	-	870	-	-	-	-	140	-	10	-	-	-	-	-	-	-	-	-	90	20	-	-	-	10	20	-	-	30	-	-	-	-	330	10	90	-
34	-	220	-	-	-	-	140	-	30	-	-	-	-	-	-	-	-	-	10	-	-	-	-	10	-	-	-	20	-	-	-	-	40	-	70	-
35	-	430	30	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	30	-	90	-	70	-	-	-	-	220	110	60	-
36	-	-	-	10	40	10	20	-	-	-	-	-	-	-	-	-	-	-	-	-	120	10	-	-	-	50	-	-	-	-	-	-	10	20	30	-
37	-	-	-	20	70	-	170	-	-	-	-	-	-	-	-	-	-	-	10	10	360	-	-	-	240	-	-	-	-	-	-	-	80	30	160	-
38	-	-	-	-	160	150	90	-	10	10	-	-	-	-	-	-	-	-	-	-	150	-	-	-	90	-	-	-	-	-	-	20	-	130	60	-
39	-	-	-	100	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	250	-	-	-	-	110	-	10	-	-	-	-	-	30	-	-
40	-	20	-	-	390	-	30	-	30	-	-	-	-	-	-	-	-	-	-	20	50	50	-	60	80	-	-	90	-	-	-	10	920	1,340	210	-
41	-	190	-	-	-	-	30	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	490	-	-	-	20	-	-	-	-	430	-	210	-
42	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-
43	-	20	-	-	10	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44	-	-	50	-	-	-	30	-	10	-	-	30	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	30	-	-
45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46	-	-	-	-	20	-	10	-	-	-	-	-	-	-	-	-	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	20
48	-	20	-	-	30	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	70	10	-
49	-	100	-	10	10	-	20	-	40	-	-	-	-	-	-	-	10	-	-	10	-	-	-	-	-	-	-	20	-	-	-	-	20	-	60	-
50	-	40	-	-	-	-	70	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	90	-	-	-	20	-	70	120	-	90	10	90	-
51	-	10	-	220	440	-	40	-	100	-	-	-	-	10	-	20	-	-	-	-	20	-	-	110	20	110	-	280	-	200	430	-	310	3,780	290	-
52	20	-	-	1,050	-	40	20	-	20	40	30	-	-	20	-	-	10	-	-	-	300	-	-	-	-	30	-	-	-	-	-	-	20	460	10	-
53	20	-	-	1,000	440	300	300	-	20	100	20	-	-	-	-	-	-	-	-	-	980	-	-	-	-	800	-	10	-	10	-	-	-	350	140	20
54	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-
55	-	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
56	80	-	-	-	880	-	240	-	-	-	80	-	-	-	-	-	-	-	-	-	80	-	-	-	-	160	-	-	-	-	-	-	80	-	-	10
57	-	10	-	800	1,440	-	80	-	10	-	-	-	40	-	-	-	-	-	10	-	180	160	-	-	-	500	-	120	-	-	-	-	240	4,600	40	-
58	-	-	-	-	150	-	80	-	130	-	-	-	-	-	-	-	-	-	-	20	10	-	20	490	-	-	-	80	10	-	-	-	430	630	200	-
59	-	20	-	-	50	-	10	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	10	30	50	-	40	-	-	80	80	10
60	-	20	60	-	390	-	30	-	170	-	-	-	-	-	-	-	-	10	-	-	-	30	-	50	-	-	-	-	70	-	240	-	30	120	70	-
61	-	10	-	10	70	-	10	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	30	-	80	30	60	-
63	-	-	50	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	10	-	-	-	-	140	-	-

Members of this group were by far the most abundant mollusks. Densities were as high as 8,230/m² (all species combined). The occurrence records of pelecypods are presented in two tables: Table 4 gives the number of shells per square meter, by stations, for the 35 more common species and Table 5 lists the number of shells per square meter for each of the 22 species that occurred at only one station. Each pelecypod shell was counted separately. No attempt was made to enumerate the left and right valves separately, because of the fragmentary nature of many specimens.

Distribution and Density

Pelecypods, all species considered, were generally most abundant in a band extending northeast-southwest across the study area and in another narrower band parallel to the depth contours near the shelf break (Figure 8). Densities were frequently less in the northwest, northeast, and south-central sections of the continental shelf and along the continental slope. As expected, the density of the group was strongly influenced by a relatively few species that were both abundant and widely distributed.

TABLE 5.—Species and density, by stations, of pelecypods that occurred at only one station each.

Species	Station	Specimens
		No/m²
Abra longicallis	21	10
Aequipecten glyptus	10	10
Anadara ovalis	16	10
Axinopsis orbiculata	8	50
Bathyarca anomala	56	80
Crenella pectinula	33	20
Cuspidaria striata	8	20
Cyrtodaria siliqua	30	20
Liocyma fluctuosa	30	10
Macoma balthica	6	10
Modiolus demissus	46	10
Myonera limatula	8	10
Mytilus edulis	1	10
Nucula delphinodonta	11	10
Nuculana tenuisulcata	38	10
Panomya arctica	25	10
Periploma affinis	4	20
Siliqua costata	17	20
Solemya velum	4	10
Tellina agilis	29	10
Thracia conradi	13	40
Thracia myopsis	5	20

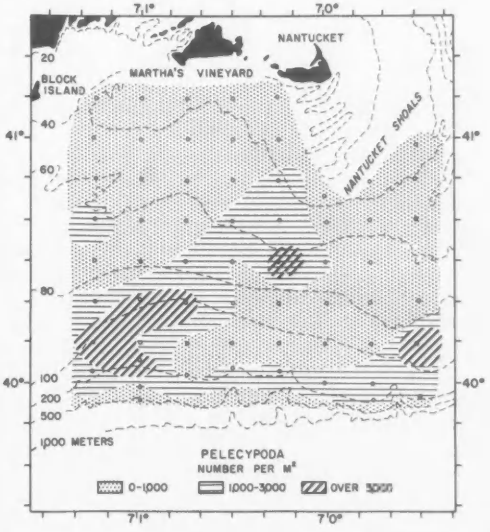

FIGURE 8.—Density distribution of pelecypod shells, all species combined.

Pelecypods were sparse (less than 50/m²) or absent at 8 stations, common (50 to 1,000/m²) at 32 stations, abundant (1,000 to 3,000/m²) at 16 stations, and very abundant (more than 3,000/m²) at 6 stations.

Pelecypod shells were present at all depths sampled (Table 6). Densities were lowest (30 to 40/m²) at both the shallowest and deepest stations; moderate (100 to 1,100/m²) between 30 and 89 m and between 200 and 249 m; high (greater than 1,100/m²) between 125 and 199 m; and highest (more than 2,000/m²) from 90 to 124 m.

TABLE 6.—Density distribution of pelecypod shells, all species combined, in relation to water depth.

Water depth class	Samples collected	Samples containing pelecypod shells	Mean number of shells
Meters	*Number*	*Percent*	*No/m²*
20-29	1	100	30
30-39	6	100	140
40-49	7	86	440
50-59	8	63	320
60-69	5	100	670
70-79	9	100	1,030
80-89	1	100	620
90-99	7	100	2,250
100-124	4	100	3,080
125-149	4	100	1,110
150-174	1	100	1,460
175-199	5	100	1,970
200-249	2	100	690
250-567	2	100	40

Relations of Density to Sediments

Pelecypods were generally more abundant in moderately fine-grained sediments than in either coarse or very fine types. Silty sand, sandy silt, and sand-silt-clay were most commonly associated with high density. Average shell density in these three substrate types ranged from 1,800 to 3,300/m². Shells were absent or sparse in gravel-sand substrates (average density 80/m²) and silts (average density 40/m²), and moderately low (average 650/m²) in sand.

Distribution and Density by Species

Geographic distributions of the 35 more common pelecypod species are illustrated in Figure 9. These charts are based on information listed in Table 4. No two species had identical distributions, but the distribution of a number of species in east-west bands across the study area suggests correlations with hydrographic features or bottom sediments, or both.

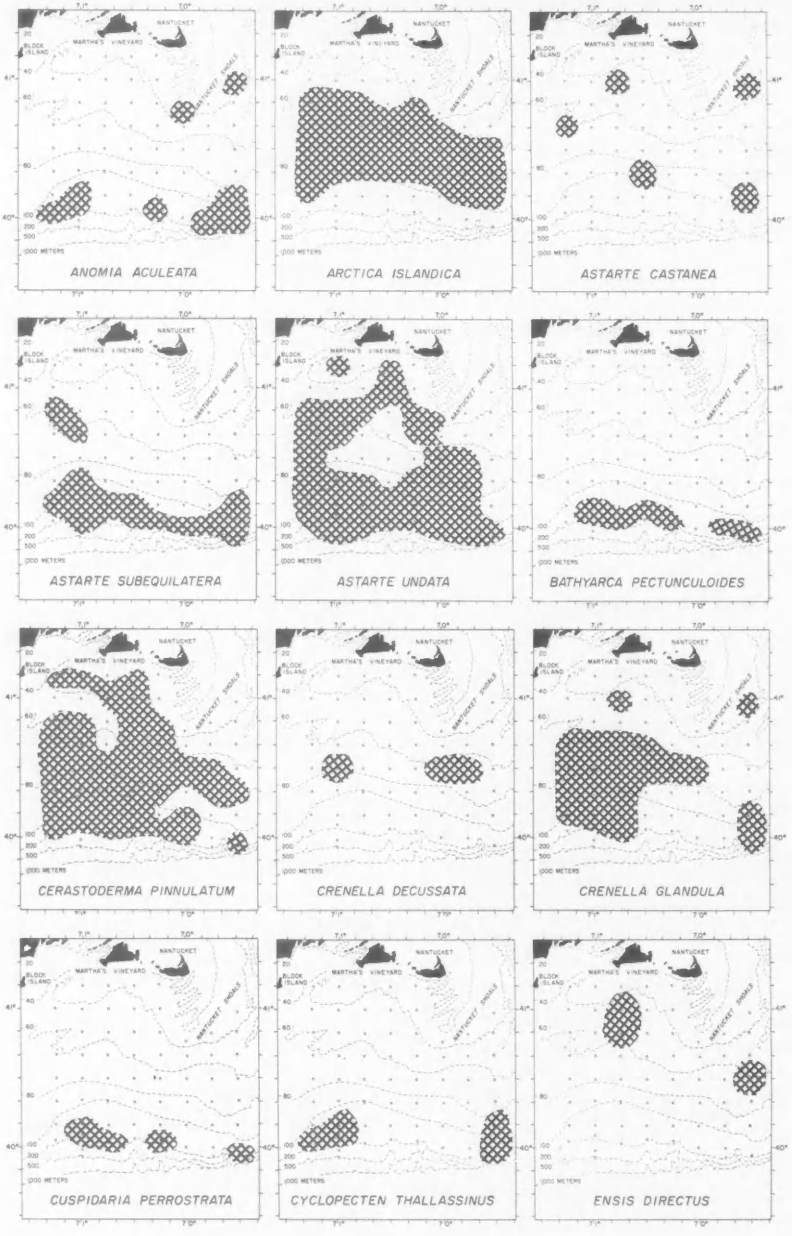

FIGURE 9.—Geographic distribution of the common pelecypods.

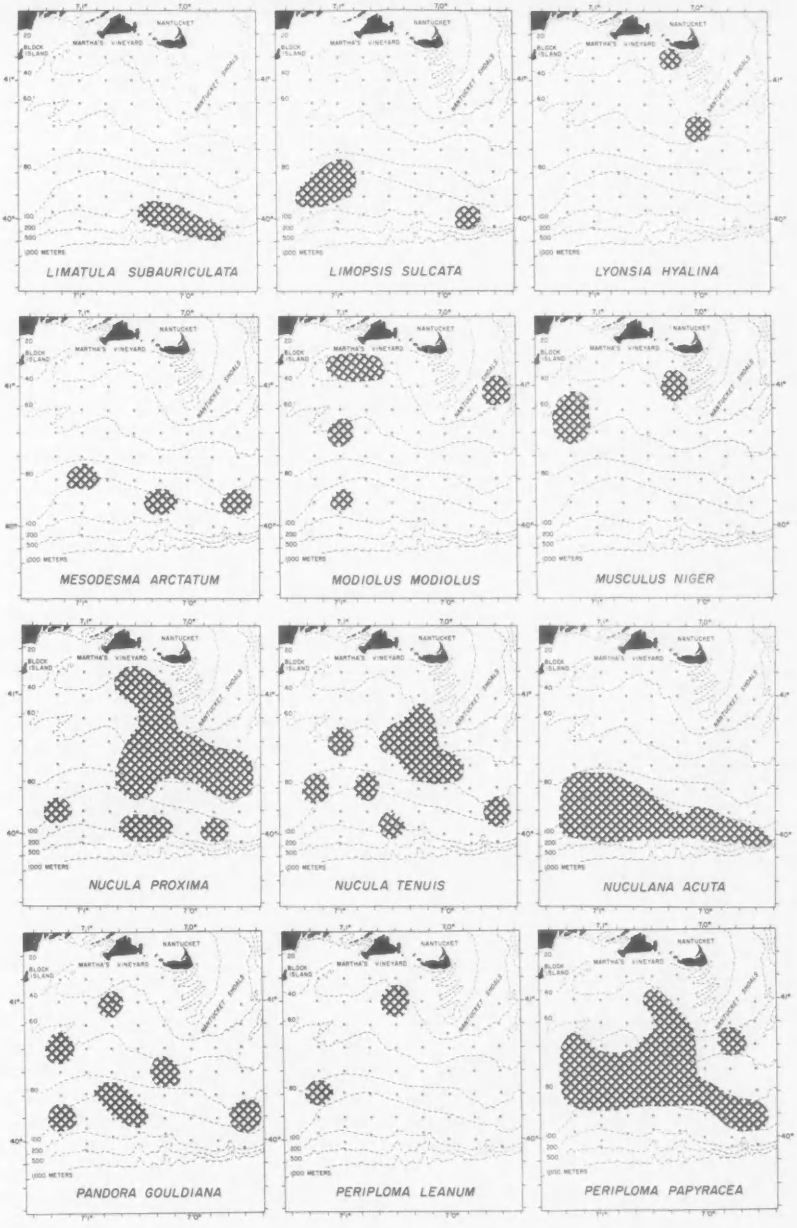

FIGURE 9.—Geographic distribution of the common pelecypods.—Continued.

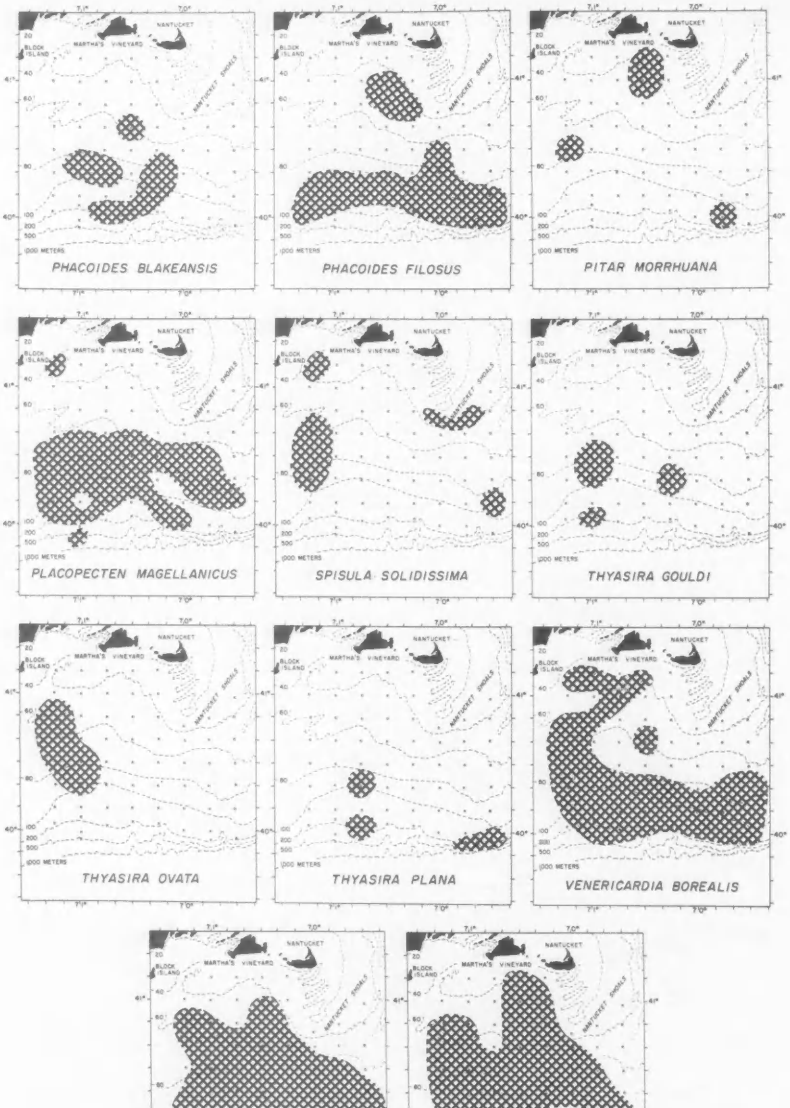

FIGURE 9.—Geographic distribution of the common pelecypods.—Continued.

The 10 most widely distributed species, in decreasing order, were: *Yoldia sapotilla, Cerastoderma pinnulatum, Astarte undata, Thyasira trisinuata, Venericardia borealis, Arctica islandica, Placopecten magellanicus, Phacoides filosus, Crenella glandula,* and *Nucula proxima.* All of these species inhabited rather broad east-west zones across the study area, except for *Nucula proxima,* which was absent in shallow water in the western sector. Its distribution was aligned in the north-south direction, and to some extent east-west.

Bathymetric distributions differed greatly among various pelecypod species. Depth range in which each species was found is listed in Table 7, and data for the most common species are plotted in Figure 10. Species dispersed over the widest depth range (38 to 567 m) were *Astarte undata* and *Placopecten magellanicus.* Depth ranges of 21 species were very narrow, but nearly all of these were based on few collections. Most of the species that occurred in two or more collections were taken over rather broad depth ranges.

Species found in shallow water (less than 50 m) were: *Anadara ovalis, Cyrtodaria siliqua, Liocyma fluctuosa, Lyonsia hyalina, Modiolus demissus, Mytilus edulis, Siliqua costata,* and *Tellina agilis.*

Species found in deep water (taken at depths greater than 200 m) were: *Anomia aculeata, Astarte subequilatera, A. undata, Cerastoderma pinnulatum, Limatula subauriculata, Nucula proxima, N. tenuis, Nuculana acuta, Phacoides blakeansis, P. filosus, Placopecten magellanicus, Thyasira plana, T. trisinuata, Venericardia borealis,* and *Yoldia sapotilla.*

Density of shells of individual pelecypod species ranged from 10/m² to 4,600/m² (Table 4). Densities tended to be high for the more widely distributed species and low for species with a restricted geographic distribution. Species found in greatest density were: *Venericardia borealis* —4,600/m², *Arctica islandica*—2,080/m², *Astarte subequilatera*—1,560/m², *Nucula proxima* —1,360/m², *Astarte undata*—1,440/m², and *Thyasira trisinuata*—1,160/m². All of these, except *Astarte subequilatera,* were among the 10 species with the widest geographic distribution. Among the species collected at 10 stations or less, few occurred in densities greater than

TABLE 7.—Bathymetric distributions of 57 species of pelecypods and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Abra longicallis	165	165	165	1
Aequipecten glyptus	139	139	139	1
Anadara ovalis	38	38	38	1
Anomia aculeata	38	201	139	10
Arctica islandica	44	110	75	27
Astarte castanea	38	97	64	5
Astarte subequilatera	62	366	152	15
Astarte undata	38	567	123	36
Axinopsis orbiculata	183	183	183	1
Bathyarca anomala	183	183	183	1
Bathyarca pectunculoides	128	194	164	7
Cerastoderma pinnulatum	38	220	96	38
Crenella decussata	73	84	77	3
Crenella glandula	46	194	99	20
Crenella pectinula	62	62	62	1
Cuspidaria perrostrata	146	194	177	5
Cuspidaria striata	183	183	183	1
Cyclopecten thallassinus	91	183	156	5
Cyrtodaria siliqua	38	38	38	1
Ensis directus	51	62	56	3
Limatula subauriculata	165	201	183	3
Limopsis sulcata	99	146	124	4
Liocyma fluctuosa	38	38	38	1
Lyonsia hyalina	27	49	38	2
Macoma balthica	91	91	91	1
Mesodesma arctatum	91	113	101	3
Modiolus demissus	40	40	40	1
Modiolus modiolus	38	146	68	5
Musculus niger	33	62	52	3
Myonera limatula	183	183	183	1
Mytilus edulis	46	46	46	1
Nucula delphinodonta	95	95	95	1
Nucula proxima	33	220	83	19
Nucula tenuis	44	220	88	10
Nuculana acuta	91	366	161	17
Nuculana tenuisulcata	194	194	194	1
Pandora gouldiana	51	110	88	7
Panomya arctica	70	70	70	1
Periploma affinis	62	62	62	1
Periploma leanum	48	91	70	2
Periploma papyracea	44	106	77	19
Phacoides blakeansis	62	220	126	7
Phacoides filosus	44	201	122	22
Pitar morrhuana	38	139	88	4
Placopecten magellanicus	38	567	116	25
Siliqua costata	49	49	49	1
Solemya velum	62	62	62	1
Spisula solidissima	37	91	62	7
Tellina agilis	27	27	27	1
Thracia conradi	73	73	73	1
Thracia myopsis	76	76	76	1
Thyasira gouldi	84	179	113	4
Thyasira ovata	62	99	77	5
Thyasira plana	106	201	171	4
Thyasira trisinuata	48	220	100	36
Venericardia borealis	38	366	116	33
Yoldia sapotilla	33	220	96	38

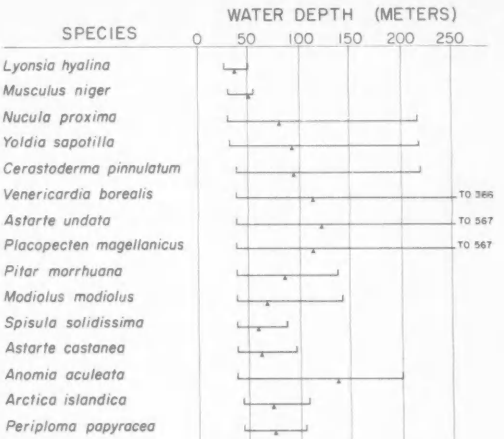

FIGURE 10.—Bathymetric range and mean depth of occurrence of the common pelecypods. (Observed values are listed in Table 7.)

500/m²; the maximum density for most of these species was less than 100/m².

Exceptions to the direct relation between high density and wide distribution were two types: (1) species widely distributed, but present in low density, such as *Cerastoderma pinnulatum, Crenella glandula, Placopecten magellanicus,* and *Yoldia sapotilla;* and (2) geographically restricted species of relatively high local densities, such as *Bathyarca pectunculoides* and *Thyasira ovata* (shells of these two species occurred at only seven and five stations each, but densities were as high as 300 and 430/m²).

Four patterns of geographic distribution revealed by these samples are: (1) Narrow band extending east-west across the area, such as: *Bathyarca pectunculoides, Crenella decussata, Cuspidaria perrostrata, Cyclopecten thallassinus, Limatula subauriculata, Mesodesma arctatum,* and *Nuculana acuta.* (2) Broad east-west band exemplified by: *Arctica islandica, Periploma papyracea, Placopecten magellanicus,* and *Thyasira trisinuata.* (3) Encircling distribution surrounding the center of the area, illustrated by *Astarte undata.* (4) Wide inshore-offshore distribution, as typified by: *Anomia aculeata, Cerastoderma pinnulatum, Crenella glandula, Nucula proxima, Venericardia borealis,* and *Yoldia sapotilla.*

Hydrographic conditions and the type of bottom sediments appear to have a substantial influence on the suitability of a habitat for some species of bivalves in this region. Unfortunately the common co-occurrence of fine-grained sediments in areas of low energy and relatively stable water temperature, as opposed to coarse sediments in high-energy and changeable water temperature does not lend itself to an evaluation of the specific conditions that limit the occurrence of the various species. Additionally, the presence of fossil shells invalidates a detailed evaluation of inferred habitat based on the presence of shell remains. For example, the shells of *Mesodesma arctatum* from depths of 91 to 113 m probably are remains of populations that inhabited nearshore areas during the rapid rise in sea level of the post-Pleistocene period. Radiocarbon age determinations for shells collected in this region at depths between 86 to 130 m, studied by Emery and Garrison (1967), range from 10,850 ± 150 to 14,850 ± 250 years before present.

Species that occurred in moderately deep waters and appeared to require a stenothermic habitat were: *Arctica islandica, Nuculana acuta, Thyasira plana,* and *Thyasira trisinuata* (Figure 9). Species that inhabited stenothermic

waters, but also showed special sediment requirements, were: *Bathyarca pectunculoides, Cuspidaria perrostrata, Limatula subauriculata,* and *Thyasira gouldi.* Conversely, those bivalves that occurred in eurythermic habitats (and coarse sediments) were: *Ensis directus, Lyonsia hyalina,* and *Musculus niger.*

Relations of pelecypod distributions with bottom sediments are discussed below.

Species-Sediment Relations

Shells from 89% of the 35 more common pelecypod species represented in the area were found in several different sediment types; only 11% were associated exclusively with one sediment type. All of the common species were primarily in sediments in which sand or silt was the chief constituent. Species frequently taken in sand sediments were: *Ensis directus, Limatula subauriculata, Lyonsia hyalina,* and *Musculus niger.* Species most commonly found in silty sand and sand were: *Bathyarca pectunculoides, Cuspidaria perrostrata, Cyclopecten thallasinus, Limopsis sulcata, Nucula proxima, N. tenuis, Nuculana acuta, Pandora gouldiana, Phacoides filosus, Pitar morrhuana, Spisula solidissima, Thyasira plana,* and *Venericardia borealis.* The only two species found mainly in sandy silt or silty sand were *Limopsis sulcata* and *Thyasira gouldi.* The absence of *Astarte undata* in the center of the area is probably due to the presence of fine-grained sediments there. All the remaining common species were collected from several different sediment types.

The presence of a narrow band of sand extending parallel to the depth contours near the outer margin of the shelf (Figure 2) appears to be a major feature affecting the distribution of many species having a narrow-band distribution (Figure 9).

GASTROPODS

Remains of gastropods formed an important component of organic origin, but compared with other mollusks they were far less common than pelecypods, but considerably more abundant than scaphopods and cephalopods. Gastropods were widely distributed throughout the area and ranged in density (all species combined) from 0 to slightly over 1,000/m². All remains were shells, except for one operculum of *Polinices duplicata.*

Forty-four species of gastropods were found in the samples. Some typical examples are shown in Figure 11. A large majority of specimens were small, less than 1 cm in shell height. Some of the smallest specimens, averaging between 2 and 5 mm, were *Alvania carinata, Cylichna alba, Retusa obtusa,* and larval forms, presumably of *Thais.* The larger species, averaging between 1 and 5 cm in greatest dimension, were: *Buccinum undatum, Colus pygmaeus, Crucibulum striatum, Crepidula fornicata,* and *Nassarius trivittatus.*

Gastropod occurrence records are listed in Tables 8 and 9. Table 8 gives the species-station record for the 24 more common species. Table 9 lists the occurrence record for species taken at only one station.

Distribution and Density

Gastropod shells (all species combined) were rather widely distributed throughout the area, occurring at 80% of the stations. Highest concentrations (250 to 1,050/m²) were in the central part of the area in a lens-shaped patch at depths between 40 and 80 m (Figure 12).

Although gastropod shells were collected at all depths, the average concentration increased in each 10-m depth class from 20 m down to about 80 m (Table 10). Concentrations were lower in deeper water, except for a zone of greater density between 175 and 250 m. *Alvania carinata* and *Cylichna gouldi* made up the bulk of the gastropod remains in the shallowwater zone: *Mitrella zonalis,* a gastropod larva, and a variety of species accounted for the high abundance in the deepwater zone.

Relations of Density to Sediments

The density of gastropod shells as a group was related to sediment type only in a rather general way. No gastropod shells were found in the coarse sand or gravel-sand substrates. Concen-

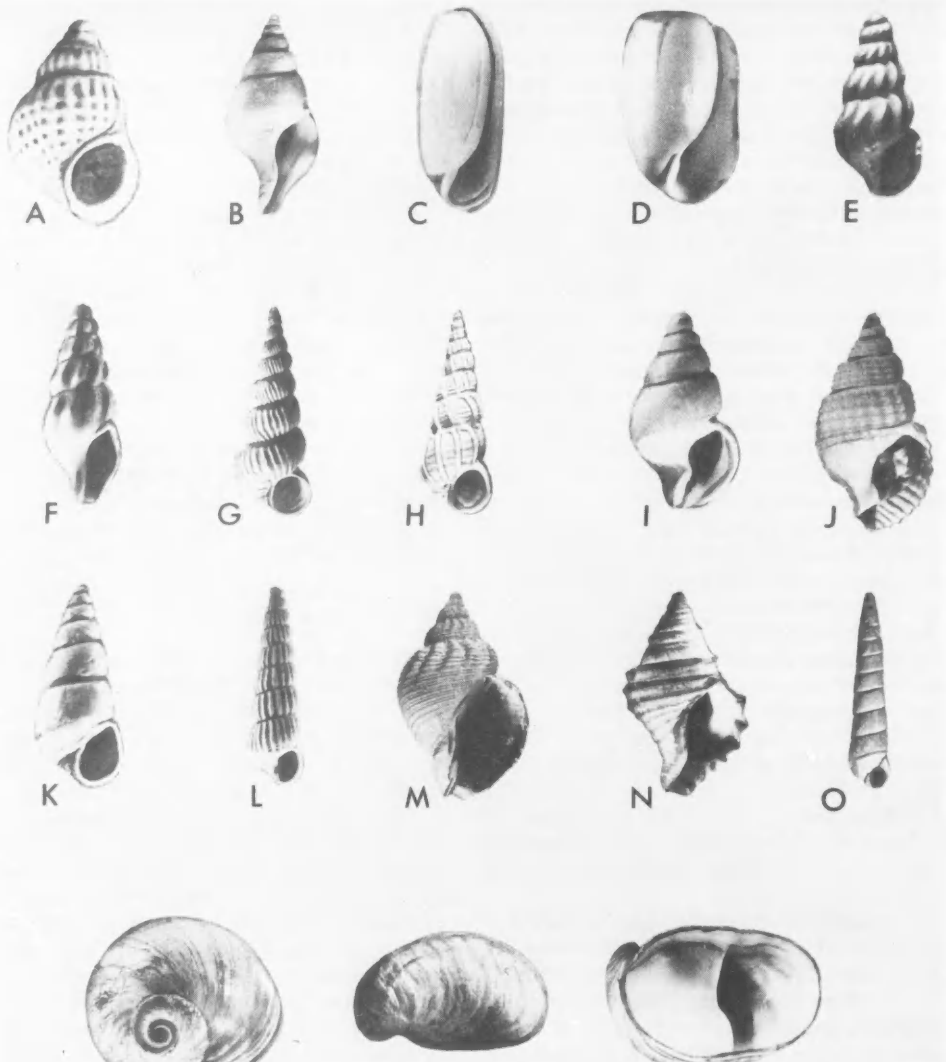

FIGURE 11.—Representative gastropods from off southeastern Massachusetts. A - *Alvania carinata* (×14); B - *Colus pygmaeus* (×1.5); C - *Cylichna alba* (×4); D - *Cylichna gouldi* (×11.7); E - *Drillia lissotropis* (×5.5); F - *Drillia* sp. (×4.7); G - *Epitonium dallianum* (×3); H - *Epitonium groenlandicum* (×0.8); I - *Mitrella zonalis* (×7); J - *Nassarius trivittatus* (×2.3); K - *Odostomia canaliculata* (×7); L - *Turbonilla interrupta* (×4.7); M - *Buccinum undatum* (×1); N - *Neptunea decemcostata* (×0.8); O - *Eulimella smithi* (×2.3); P - *Polinices duplicata* (×1); Q - *Crepidula fornicata* (×0.8); R - *Crepidula fornicata* (×0.8).

Table 8.--Species and density (number per square meter), by station, of the common gastropods.

Station number	Alvania carinata	Anachis costulata	Balcis intermedia	Buccinum undatum	Colus pygmaeus	Crepidula fornicata	Cruciblulum striatum	Cylichna alba	Cylichna gouldi	Drillia lissotropis	Epitonium dallianum	Epitonium novangliae	Lunatia levicula	Mitrella zonalis	Mitrella sp.	Nassarius trivittatus	Odostomia canaliculata	Polinices duplicata	Rissoa sp.	Trochidae	Turbonilla interrupta	Turbonilla sp.	Gastropod larva	Unidentified
4	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	-	-	-
6	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-
8	20	-	20	-	-	-	-	-	20	-	-	10	-	50	-	-	10	-	-	-	-	-	-	-
9	-	30	-	-	-	-	-	-	-	10	40	-	-	-	-	-	-	-	-	-	50	-	10	-
10	-	-	10	-	-	-	-	-	-	-	10	-	-	20	-	-	-	-	-	10	40	10	-	-
11	60	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	20	-	-	-	-	20	-	-	20	-	-	-	-	-	-	-
13	-	-	-	-	60	-	-	-	10	-	-	-	-	-	-	-	10	-	30	-	-	-	-	-
14	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-
15	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	40	-	10	-	-	-	-	-	-
17	-	-	-	-	40	-	-	10	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-
18	200	-	-	-	10	-	-	-	100	-	-	-	-	40	-	-	30	-	-	-	10	-	10	20
19	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	10	-
20	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	10	-	-	-	-	-	-	-	-	-	-	-	-	30	-	-	-	-	-	-	-	-	10	-
22	-	-	-	-	-	-	-	10	-	-	10	-	-	10	-	-	10	-	-	-	10	-	20	-
23	20	-	-	-	-	-	-	-	-	20	-	-	-	10	-	-	-	-	-	-	50	-	10	-
24	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	630	-	-	-	10	-	-	-	410	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	-	-	-	-	-	-	-	-	530	-	-	-	-	-	-	20	-	-	-	-	-	10	-	-
27	-	-	-	-	-	10	-	-	70	-	-	-	-	-	-	130	-	-	-	-	-	-	-	-
28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-
30	-	-	-	-	20	-	-	-	10	-	-	-	-	-	-	50	-	10	-	-	-	-	-	-
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32	90	-	-	10	-	-	-	-	40	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-
33	600	-	-	-	10	-	-	-	150	-	-	-	-	20	-	10	-	-	-	-	-	-	-	-
34	40	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-
35	80	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	20	-
36	50	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	10	-	-	-	-	-	30	-
37	10	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	10	-	-	-	-	-	30	-
38	10	-	-	-	-	-	-	10	-	10	30	-	-	20	10	-	-	-	10	-	10	-	-	-
40	20	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-
41	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42	10	-	-	-	-	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	30	10	-	-	-	-	-	-	-
49	-	-	-	-	-	-	-	-	80	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-
51	10	-	-	-	-	-	-	-	-	-	10	-	-	10	-	-	-	-	-	-	-	-	-	10
52	-	-	10	10	-	-	10	-	-	-	30	-	-	-	-	-	20	-	-	-	10	-	-	-
53	10	-	-	-	-	-	-	10	-	-	20	-	-	30	10	-	-	-	-	-	-	-	-	10
54	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	30	-
55	-	10	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	40	-
56	-	-	-	-	-	-	-	-	-	10	-	-	-	10	-	-	-	-	-	-	20	-	-	-
57	-	-	10	-	-	-	-	-	-	-	50	-	-	-	-	-	10	10	-	-	-	-	-	-
58	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	10	-	-	-	-	-	10	-	-	-	-	10	-	-	-	-	-
61	10	-	-	-	10	-	-	30	10	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
62	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
63	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	20	-	-	-	-	-	-	-	-

trations were high in silty sand in some areas but were intermediate or low in other locations at similar depths. Densities of gastropod shells were high, intermediate, and low in sand, with no apparent correlation.

Distribution and Density by Species

The geographic distributions of the 24 most common forms of gastropods are shown in Figure 13. These charts are based on the data in

TABLE 9.—Species and density, by station, of gastropods that occurred at only one station each.

Species	Station	Specimens
		No/m²
Alvania jannayeni	55	20
Calliostoma occidentalis	23	20
Calliostoma sp.	53	10
Cavolina longirostris	51	10
Cavolina tridentata	53	20
Epitonium groenlandicum	52	10
Epitonium multistriatum	23	30
Eulimella smithi	37	10
Eulimella sp.	6	20
Eupleura caudata	29	10
Fossarus elegans	52	10
Lunatia heros	1	10
Mitrella lunata	27	10
Neptunea decemcostata	31	10
Odostomia gibbosa	1	40
Pseudorotella solida	38	40
Pyramidella sp.	21	10
Retusa obtusa	5	40
Solariella iris	9	30
Taranis cirrata	9	10
Turrtellopsis acicula	37	10

TABLE 10.—Density distribution of gastropod shells, all species combined, in relation to water depth.

Water depth	Samples collected	Samples containing gastropod shells	Mean number of shells
Meters	*Number*	*Percent*	*No/m²*
20-29	1	100	10
30-39	6	83	35
40-49	7	71	84
50-59	8	63	96
60-69	5	100	190
70-79	9	89	221
80-89	1	0	0
90-99	7	100	51
100-124	4	100	72
125-149	4	75	80
150-174	1	100	60
175-199	5	100	102
200-249	2	100	140
250-567	2	100	65

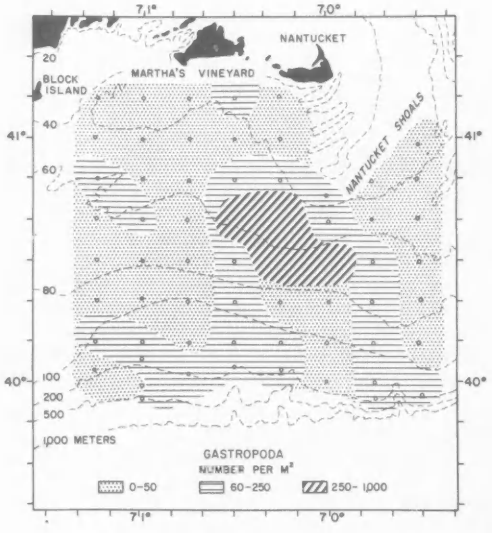

FIGURE 12.—Density distribution of gastropod shells, all species combined.

Table 8. Species with a wide geographic distribution were, in decreasing order: *Alvania carinata, Mitrella zonalis, Cylichna gouldi, Colus pygmaeus, Odostomia canaliculata, Epitonium dallianum, Cylichna alba, Nassarius trivittatus,* and *Turbonilla interrupta.*

Four patterns of geographical distribution are revealed: (1) The most common is a relatively narrow east-west band across the area in either shallow or deep water, typified by *Balcis intermedia, Crepidula fornicata, Drillia lissotropis, Epitonium dallianum,* and others. (2) Comparatively broad east-west bands across the area are illustrated by *Mitrella zonalis* and *Turbonilla interrupta.* (3) Peripherial occurrence around the fine-grained bottom sediments located in the center of the area is illustrated by *Cylichna alba, Odostomia canaliculata,* and to some extent by *Rissoa* sp. (4) Distribution in the central part of the area, a pattern nearly opposite that of peripheral distribution (pattern number 3), is illustrated by *Alvania carinata.*

Bathymetric range differed markedly among species. The minimum, maximum, and mean depth of occurrence for each species is listed in Table 11 and illustrated for the more common species in Figure 14. *Mitrella zonalis* was the only species taken over a wide range of water depths (62 to 567 m). Species that had a moderately wide depth range were: *Buccinum undatum, Cylichna alba, Epitonium novangliae, Odostomia canaliculata,* and *Rissoa* sp.

Species found in shallow water—those restricted to depths of 50 m or less—were: *Crepidula fornicata, Eupleura caudata, Lunatia her-*

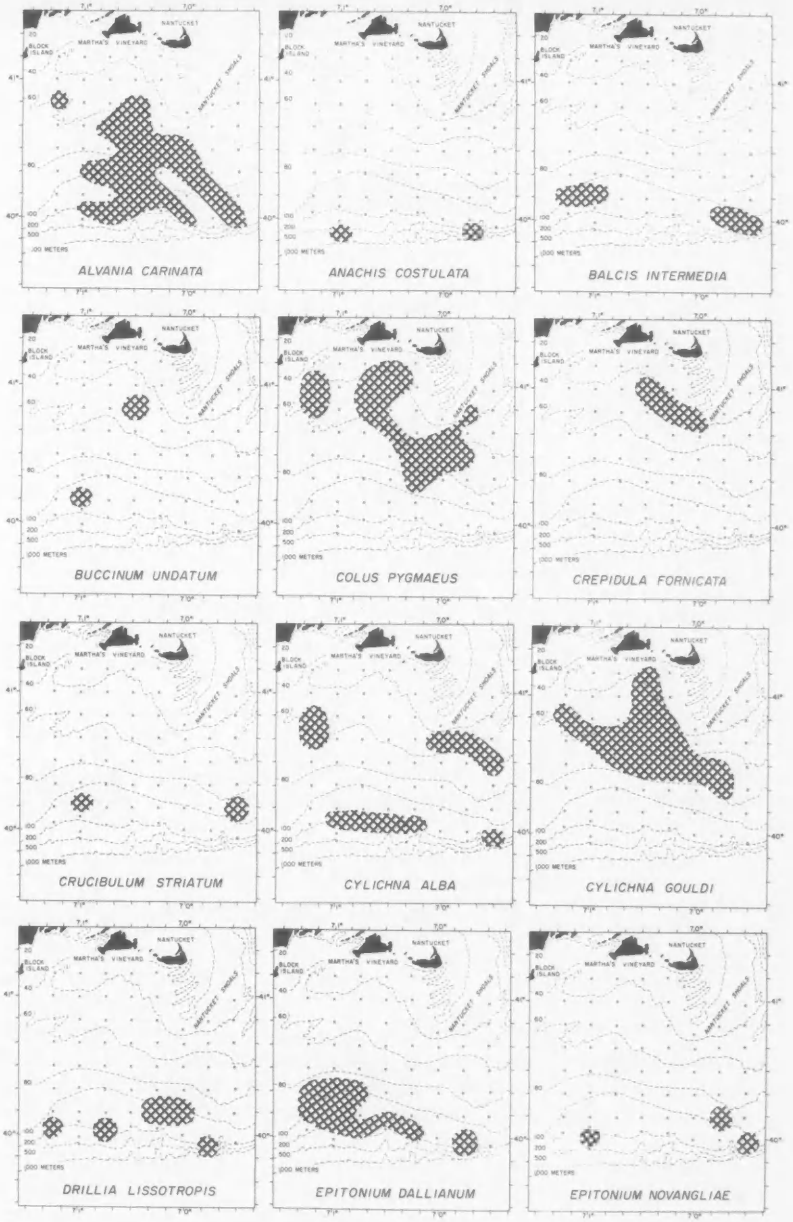

FIGURE 13.—Geographic distribution of the common gastropods.

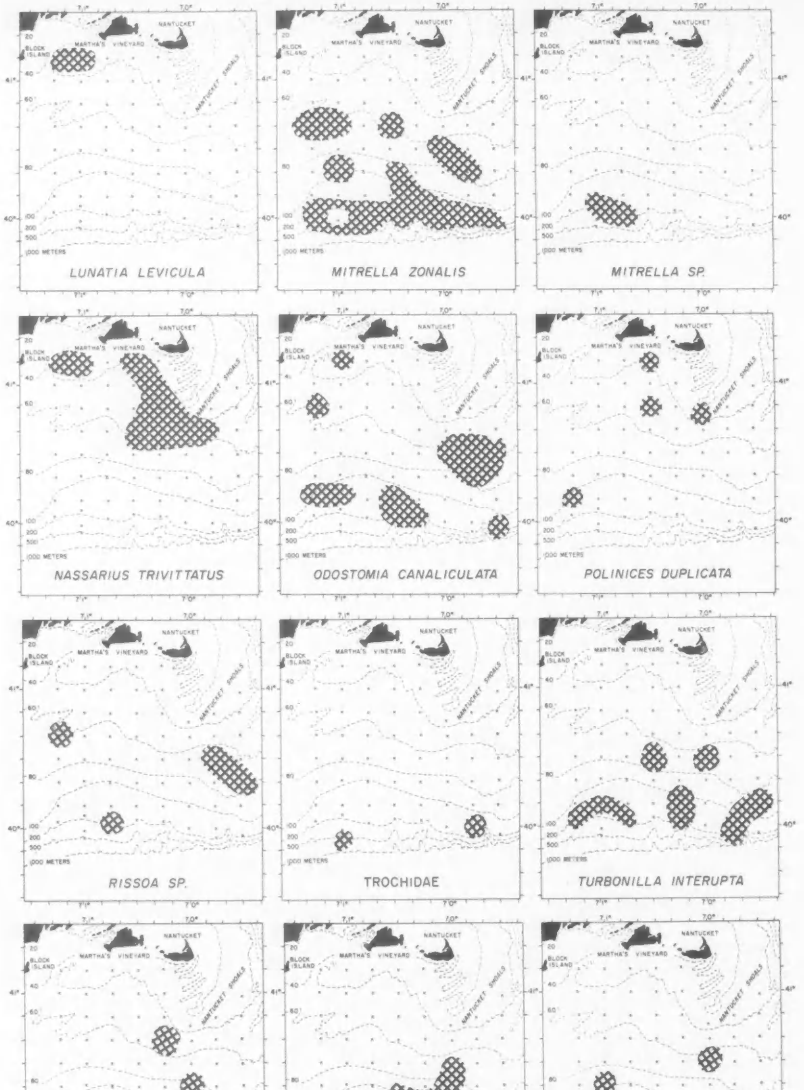

FIGURE 13.—Geographic distribution of the common gastropods.—Continued.

TABLE 11.—Bathymetric distributions of 44 gastropods and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Alvania carinata	59	220	112	19
Alvania janmayeni	567	567	567	1
Anachis costulata	201	567	384	2
Balcis intermedia	110	183	144	4
Buccinum undatum	59	146	102	2
Calliostoma occidentalis	113	113	113	1
Calliostoma sp.	179	179	179	1
Cavolina longirostris	99	99	99	1
Cavolina tridentata	179	179	179	1
Colus pygmaeus	37	90	58	13
Crepidula fornicata	38	48	43	3
Crucibulum striatum	91	146	118	2
Cylichna alba	49	220	125	10
Cylichna gouldi	38	79	63	15
Drillia lissotropis	113	201	162	5
Epitonium dallianum	91	201	143	11
Epitonium groenlandicum	146	146	146	1
Epitonium multistriatum	113	113	113	1
Epitonium novangliae	95	366	215	3
Eulimella smithi	220	220	220	1
Eulimella sp.	91	91	91	1
Eupleura caudata	27	27	27	1
Fossarus elegans	146	146	146	1
Lunatia heros	46	46	46	1
Lunatia levicula	38	40	39	2
Mitrella lunata	44	44	44	1
Mitrella zonalis	62	567	157	17
Mitrella sp.	179	194	186	2
Nassarius trivittatus	33	62	45	10
Neptunea decemcostata	48	48	48	1
Odostomia canaliculata	40	220	113	12
Odostomia gibbosa	46	46	46	1
Polinices duplicata	38	110	61	4
Pseudorotella solida Dall	194	194	194	1
Pyramidella sp.	165	165	165	1
Retusa obtusa	76	76	76	1
Rissoa sp.	62	194	101	4
Solariella iris	201	201	201	1
Solariella sp.	139	139	139	1
Taranis cirrata	201	201	201	1
Turbonilla interrupta	73	201	140	10
Turbonilla sp.	51	139	70	3
Turrtellopsis acicula	220	220	220	1
Gastropod larva[1]	73	567	200	11

[1] Only one species appeared to be represented—possibly a *Thais*.

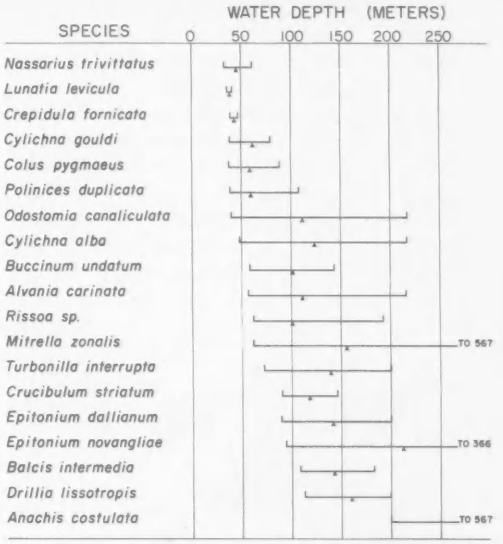

FIGURE 14.—Bathymetric range and mean depth of occurrence of the more common gastropod species. (Observed values are listed in Table 11).

os, *L. levicula*, *Mitrella lunata*, *Neptunea decemcostata*, and *Odostomia* sp.

Species taken only in deep water—those restricted to depths greater than 200 m—were: *Alvania janmayeni*, *Anachis costulata*, *Eulimella smithi*, *Taranis cirrata*, and *Turrtellopsis acicula*. All these species were taken at only one station, except *Anachis costulata*, which occurred at two stations.

Shells of individual species of gastropods generally occurred at low or moderately low densities. Only three were found in high or moderately high concentrations: *Alvania carinata* (630/m²), *Cylichna gouldi* (530/m²), and *Nassarius trivittatus* (130/m²). The density of other gastropods (41 species) was 60/m² or less.

Species-Sediment Relations

The majority of gastropod species occurred in sand and silty sand. None was in coarse sand or gravel-sand substrates, and none appeared to be restricted to silt. Widely distributed species generally occurred in a variety of sediment types ranging from medium sand to silt. A few species were associated with specific sediment types. Gastropods found chiefly in sand substrates were: *Colus pygmaeus*, *Crepidula fornicata*, *Cylichna alba*, *Lunatia levicula*, *Nassarius trivittatus*, and *Odostomia canaliculata*. The only species found principally in fine-grained sediments was *Epitonium dallianum;* it was mainly in silty sand.

CEPHALOPODS AND SCAPHOPODS

Remains of cephalopods and scaphopods were found in moderate to low densities, were small, and occurred in a relatively limited area. Only a few species of each group were represented in the samples. Illustrations of typical examples are shown in Figure 15.

Cephalopod remains consisted solely of beaks (jaws or mandibles) of Decapoda (squid). All were black and 4 to 6 mm long. The animals from which the beaks came were adults and probably rather small (less than about 10 cm in mantle length). Their uniformity in configuration and size suggests that only one or a few species are represented.

Scaphopod remains consisted only of shells or fragments of shells of a few species of the genus *Dentalium* (15 to 35 mm long) and one species of the genus *Cadulus* (mostly 10 to 13 mm long). Many *Dentalium* shells were inhabited by Sipunculida, whereas *Cadulus* shells were empty. Unbroken shells recovered from the samples included few of the thin-walled *Cadulus* but larger numbers of the thick-walled *Dentalium*.

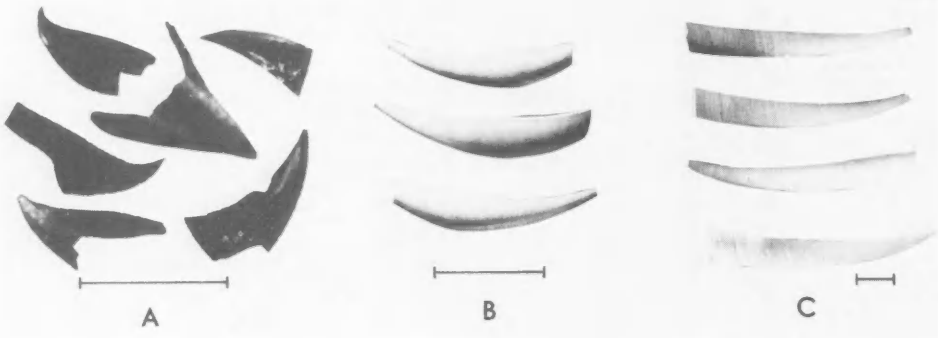

FIGURE 15.—Cephalopod mandibles and scaphopod shells from off southeastern Massachusetts. A - cephalopod beaks; B - shells of *Cadulus pandionis*; C - shells of *Dentalium* spp. Each scale bar is 5 mm.

TABLE 12.—Density of cephalopod beaks and scaphopod shells, by stations.

Station	Cephalopods[1]	Scaphopods	
		Cadulus pandionis	*Dentalium* spp.
	No/m²	*No/m²*	*No/m²*
5	10	--	--
6	--	--	--
8	40	--	20
9	--	80	--
10	10	10	--
11	10	--	--
21	30	--	20
22	--	20	20
23	20	--	110
36	20	--	--
37	40	110	--
51	--	--	40
53	20	60	10
54	130	10	--
55	110	--	--
56	10	--	--
57	--	--	10

[1] Remains of mandibles.

Distribution and Density

The distribution of cephalopod and scaphopod remains was somewhat limited geographically and densities were low. Quantitative occurrence records for both groups (Table 12), geographic distributions (Figures 16 and 17), and depth of water inhabited (Table 13), disclose that both groups occur primarily in deep water, only on the continental slope and outer part of the shelf.

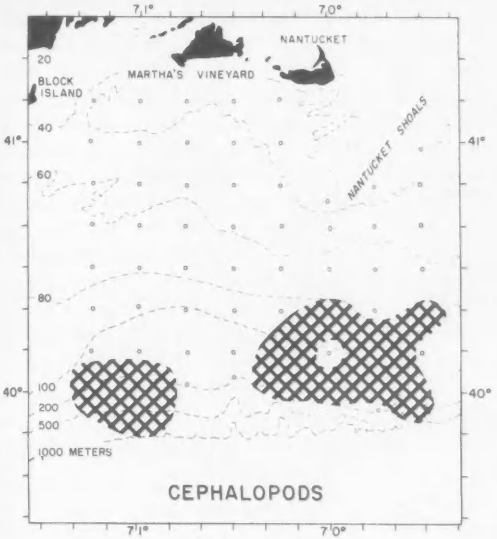

FIGURE 16.—Geographic distribution of cephalopod beaks.

Cephalopod beaks were present at 12 stations, at a depth range of 76 to 567 m. Their average density was 38/m², and maximum density 130/m². Highest densities were at the deepest stations sampled, stations 54 and 55, where water depths were 366 and 567 m.

Scaphopod shells were collected at 11 stations. *Cadulus pandionis* was present only on the continental slope at depths between 139 and 366 m. Average density at the six stations where it occurred was 41/m² and maximum density was 110/m². *Dentalium* spp. occurred along the continental shelf margin at depths of 91 to 183 m.

TABLE 13.—Bathymetric distribution of cephalopod beaks and scaphopod shells and the number of stations at which each occurred.

Species	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Cephalopods	76	567	201	12
Scaphopods				
Cadulus pandionis	139	366	213	6
Dentalium spp.	91	183	134	7

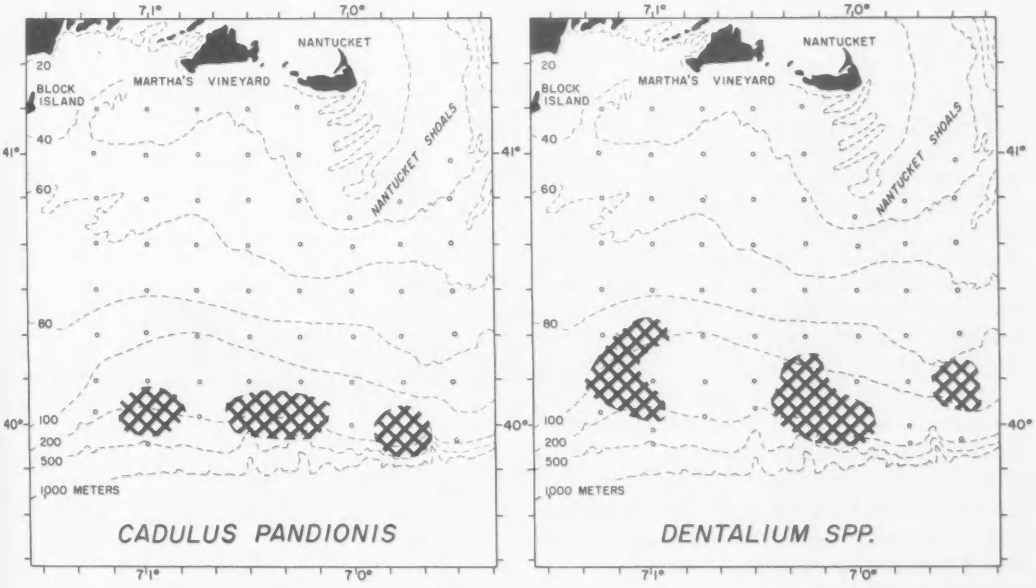

FIGURE 17.—Geographic distribution of shells of the scaphopods, *Cadulus pandionis* and *Dentalium* spp.

Average density at seven stations was 33/m², and maximum density was 110/m².

Relations with Sediments

The kinds of cephalopods that are abundant in this region are pelagic and their occurrence would not ordinarily be expected to be directly related to substrate composition. The fate of the remains of these animals that drop to the ocean floor may depend indirectly on sediment type because these species generally occur in deep or moderately deep water. Cephalopod remains were absent in coarse sand or gravel. Densities were moderate (10 to 40/m²) exclusively in silt.

Cadulus and *Dentalium* remains also were found only in fine-grained sediments; fine sand, silty sand, sandy silt, and silt. No areas of coarse sand, gravel, or mixtures of the two yielded scaphopod shells. A large majority were in areas where the sediments are fine sand and silty sand. *Cadulus* was densest in fine sand, and *Dentalium* in silty sand.

REMAINS OF FISH

Vertebrate remains in the bottom sediments were represented exclusively by fish otoliths and small numbers of bones, teeth, and scales (Table 14). Some examples of typical otoliths are illustrated in Figure 18. Otoliths were rather broadly distributed over much of the area but were particularly common in the deepwater section. The otolith density was strikingly high, 3,020/m², near the shelf break south of Nantucket Shoals. All samples combined included 18 genera and at least 26 species of fish; all but one were identified from otoliths. A record of the otoliths of each species recovered at different stations is given in Table 15. Eleven of the species are bottom-dwelling types, and 11 are epipelagic or mesopelagic (Table 16). Three species, *Merluccius albidus*, *M. bilinearis*, and *Peprilus triacanthus*, represented by otoliths range widely from the sea bottom to upper water levels; they remain unclassified for the purposes of this discussion. Clupeoids, scombroids, and other common pelagic groups were lacking. The collections included many more otoliths from pelagic species (1,288), however, than from groundfish (141); the average otolith density (based only on samples containing one or more otoliths), of pelagic species was 379/m², compared with 41/m² for groundfish. All fish remains were less than 2 cm in greatest dimension, and most were less than 3 mm. The sizes of fish from which these remains came ranged from lanternfish only a few centimeters long to sharks estimated to be 2 to 3 m long.

TABLE 14.—Density of fish remains[1], all species combined, by stations.

Station number	Otoliths	Bones
	No/m²	*No/m²*
4	10	--
5	10	--
6	30	--
8	3,020	--
9	1,250	--
10	360	10
11	10	20
12	10	--
13	--	10
16	--	10
17	10	--
18	--	10
20	20	--
21	760	10
22	2,200	10
23	170	40
24	--	10
25	--	30
27	30	10
31	10	--
33	10	--
34	10	10
35	40	10
36	30	10
37	1,460	80
38	1,270	--
39	150	10
40	20	10
41	20	20
50	--	60
51	50	10
52	50	--
53	830	--
54	870	40
55	580	--
56	1,380	--
57	60	10
58	10	--
59	10	--
61	10	--

[1] Scales occurred only at stations 11, 17, and 40 (10 to 20/m²) and teeth only at stations 53 and 54 (20 to 30/m²).

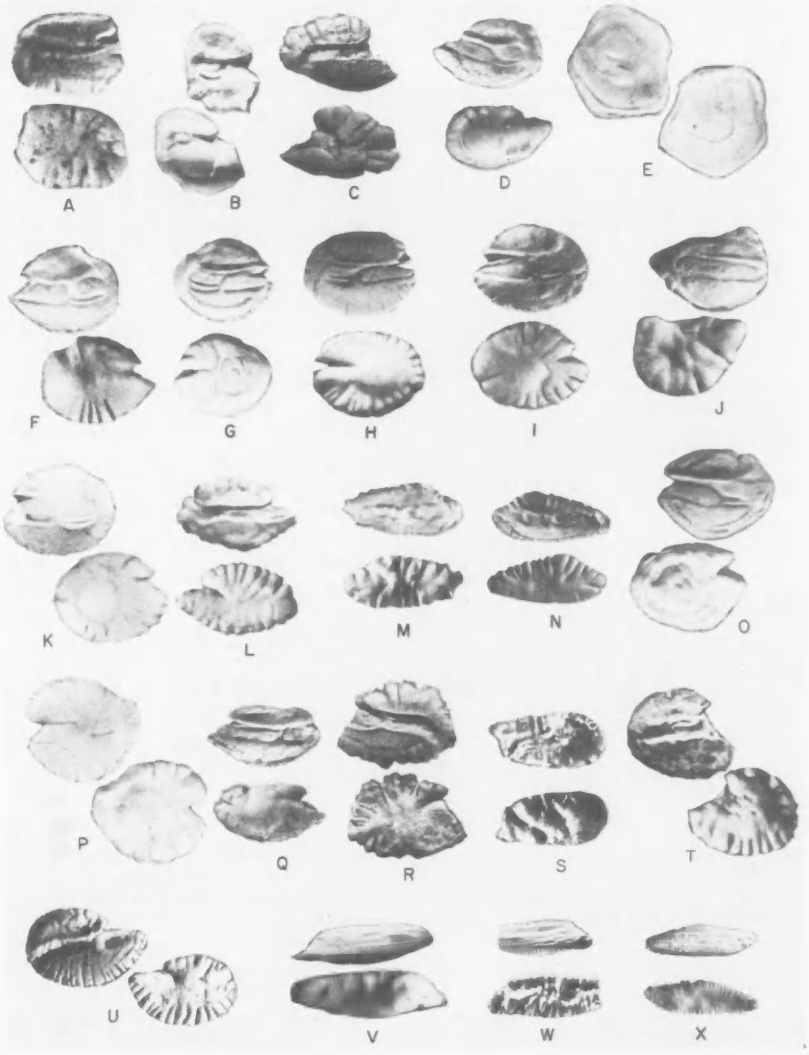

FIGURE 18.—Representative teleost otoliths from off southeastern Massachusetts. Inner face of otolith above, outer face below. A - Acanthuroidei sp.-1 (×10); B - *Benthosema glaciale* (×6.5); C - *Centropristis ocyurus* (×8); D - *Ceratoscopelus maderensis* (×4.5); E - *Citharichthys ?arctifrons* (×9); F - *Diaphus* sp.-1 (×2); G - *Diaphus* sp.-2 (×4.5); H - *Diaphus* sp.-3 (×4); I - *Diaphus* sp.-4 (×6.5); J - *Lepophidium cervinum* (×5.2); K - *Lobianchia dofleini* (×7); L - *Lopholatilus chamaeleonticeps* (×2.5); M - *Merluccius albidus* (×4.5); N - *Merluccius bilinearis* (×2); O - *Myctophum punctatum* (×4.5); P - *Myctophum* sp. (×6.5); Q - *?Notoscopelus* (×3.2); R - *Peprilus triacanthus* (×4.5); S - *Phycis chesteri* (×5.8); T - *Pomacanthus arcuatus* (×10); U - *"Stromateus"* (×5.8); V - *Urophycis chuss* (×2); W - *Urophycis ?floridanus* (×2); X - *Urophycis tenuis* (×1.3).

Table 15.--Species and density (number per square meter) of fish otoliths, by station.

Station number	Acanthuroidei sp.-1	Acanthuroidei sp.-2	Benthosema glaciale	Centropristis ocyurus	Ceratoscopelus maderensis	Citharichthys ?arctifrons	Diaphus sp.-1	Diaphus sp.-2	Diaphus sp.-3	Diaphus sp.-4	Lepophidium cervinum	Lobianchia dofleini	Lopholatilus chamaeleonticeps	Merluccius albidus	Merluccius bilinearis	Merluccius sp.	Myctophum punctatum	Myctophum sp.	?Notoscopelus	Peprilus triacanthus	Phycis chesteri	Pomacanthus arcuatus	"Stromateus"	Urophycis chuss	Urophycis ?floridanus	Urophycis tenuis	Urophycis sp.	Unidentified fragments
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	+
8	-	-	40	20	2,160	130	-	180	-	270	40	10	-	-	40	-	-	120	-	10	-	-	-	-	-	-	-	-
9	-	-	-	-	650	-	-	30	-	440	10	10	-	-	-	-	10	80	-	-	10	-	-	-	-	10	-	-
10	-	-	-	-	220	20	-	-	-	30	50	-	-	-	20	-	10	10	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	-	-	-	-	520	40	-	20	-	110	40	-	-	-	-	-	10	20	-	-	-	-	-	-	-	-	-	-
22	-	-	10	-	1,480	110	-	20	-	330	80	-	-	-	60	-	10	70	10	-	-	-	-	10	-	10	-	-
23	-	-	-	-	40	50	-	-	-	-	30	-	10	-	-	20	-	-	-	-	-	-	-	10	10	-	-	-
27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	10	-	-	-	-	-
31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
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38	-	-	-	-	970	40	-	-	10	110	40	10	-	-	50	-	-	20	10	-	-	-	-	10	-	-	-	-
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51	-	-	-	-	10	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
52	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53	10	10	-	-	460	50	-	20	-	160	80	-	-	-	20	-	-	20	-	-	-	-	-	-	-	-	-	-
54	-	-	10	-	820	-	-	-	-	20	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-
55	-	-	10	-	500	20	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
56	-	-	20	-	1,010	30	100	-	10	-	110	-	-	-	10	-	10	20	20	-	-	-	-	-	-	40	-	-
57	-	-	-	10	10	10	-	10	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	+
59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 16.—Comparison of density and abundance of otoliths of pelagic fish and groundfish.

Item	Pelagic	Groundfish	Unclassified
Number of otoliths	1,288 (87%)	141 (10%)	41 (3%)
Average otolith density (per m²)			
Including all samples (62)	208	23	7
Only samples with otoliths (34)	379	41	12
Number of species	11 (44%)	11 (44%)	3 (12%)

IDENTIFICATION OF OTOLITHS

Otoliths of relatively deepwater teleosts form the major portion of all species dealt with here; littoral species rarely occurred in the samples. Myctophids (lanternfishes) contributed most of the otoliths. Many of these have been referred tentatively to various genera in this group, but specific determinations are not possible in the absence of suitable identified material for comparison. It is very likely that the species are already in ichthyological collections, but most

preserving fluids soon render the otoliths useless, if they do not destroy them completely.

Nearly all the otoliths had suffered some erosion that may have resulted from abrasion on the sea bottom, possibly preceded by partial dissolution in the digestive system of predatory animals and later by the reworking of bottom sediments by deposit-feeding benthic invertebrates such as polychaete worms, holothurians, starfish, and many others. One or several of these agents resulted in the destruction of the rostral area on all percoid otoliths. The outer rims of some merluccid otoliths were damaged sufficiently to make identification difficult.

DISTRIBUTION AND DENSITY

Fish remains, all species combined, occurred at 65% of the stations. The remains were not uniformly distributed over the area but occurred mainly in the southern, offshore sector (Figures 19 and 20). More than 90% of all fish remains were taken at depths greater than 150 m, whereas less than 1% came from depths less than 50 m. Only 36% of the samples collected at depths less than 100 m contained one or more otoliths, whereas all samples taken at depths greater than 100 m contained otoliths (Table 17). Highest densities, 500 to 3,030/m², were in a band parallel to the isobaths along the outer portion of the continental shelf and upper part of the continental slope.

Density of fish otoliths was correlated closely

TABLE 17.—Density distribution of fish otoliths in relation to water depth.

Water depth	Samples collected	Samples containing otoliths	Mean number of otoliths
Meters	*Number*	*Percent*	*No/m²*
20-29	1	0	0
30-39	6	0	0
40-49	7	43	7
50-59	8	0	0
60-69	5	60	6
70-79	9	56	7
80-89	1	0	0
90-99	7	71	20
100-124	4	100	70
125-149	4	100	142
150-174	1	100	740
175-199	5	100	1,724
200-249	2	100	1,365
250-567	2	100	735

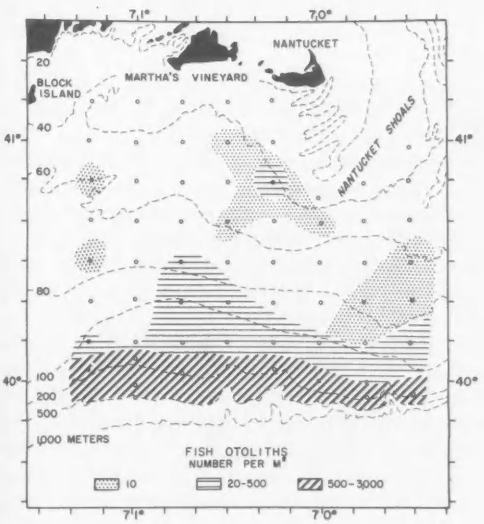

FIGURE 19.—Geographic distribution and density of fish otoliths, all species combined.

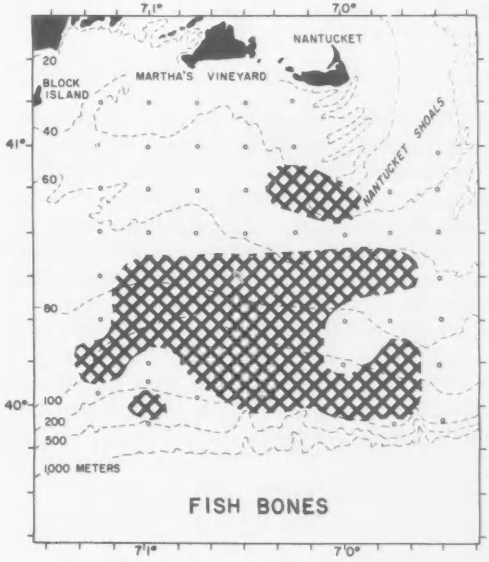

FIGURE 20.—Geographic distribution of fish bones.

with water depth (Table 17). Average densities ranged from 0 to 20/m² between 20 and 100 m and from 735 to 1,724/m² between 150 and 567 m.

Environmental features that contributed substantially to the observed correlations are the low energy environment combined with the relatively mild abrasive characteristics of the bottom sediments.

Densities of fish teeth, bones, and scales were low (80/m² or less). Teeth were recovered at only two stations (53 and 54), where water depths were 179 and 366 m; densities were 20 to 30/m². The teeth at station 53 were from the blue shark, *Prionace glauca*, a cosmopolitan species that commonly attains lengths of 2 to 3 m. Fish scales were found at three stations, at water depths of 49 to 106 m, and at densities of 10 to 20/m². Fish bones were detected at 22 stations (Figure 20). Vertebrae and rib bones were encountered most frequently but occasionally skeletal sections from the oral and branchial regions were taken. The small thin bones generally had a fresh appearance, whereas the larger thicker bones were often badly eroded and stained brown. Fish bones were collected at water depths from 38 to 366 m; densities ranged from 10 to 80/m².

RELATIONS OF DENSITY TO SEDIMENTS

A broad comparison of the geographic distribution and density of fish remains (Figures 19 and 20) with bottom sediment types (Figure 2) disclosed a moderately close correlation. The most obvious aspects were the absence of fish remains in gravel-sand mixtures, and an exceedingly low density in coarse and medium sand sediments. Conversely, fish remains were comparatively common in silt, sandy silt, and fine-grained sand. Otoliths had highest densities in the fine sand, whereas bones were common in sediments composed chiefly of silt and clay with admixtures of fine sand.

DISTRIBUTION AND DENSITY BY SPECIES

Of the 26 fish species whose remains were recovered from the bottom sediments, only six were abundant or moderately abundant; *Ceratoscopelus maderensis*, *Citharichthys ?arctifrons*, *Diaphus* sp.-4, *Lepophidium cervinum*, *Merluccius bilinearis*, and *Myctophum* sp. (Fish species represented by otoliths are listed by station in Table 15.) Each of these species occurred at eight or more stations, and maximum densities ranged from 60 to 2,160/m². Four of the six abundant species are pelagic forms (exceptions are *L. cervinum* and *M. bilinearis*, although *M. bilinearis* frequently is mesopelagic). The most common species was *Ceratoscopelus maderensis*. Otoliths of this species occurred at 19 stations and average density was 530/m².

Nearly all fish remains were collected in the southern half of the area. The geographic distribution of otoliths of different species is illustrated in Figure 21. With few exceptions, otoliths of individual species were geographically distributed in an east-west band across the area, roughly parallel to the depth contours. A major exception to this distribution was that for *M. bilinearis*, the most widely distributed species. It was found at 15 stations, most of which were located on the outer continental shelf, but a few otoliths occurred on the central and inner portions of the shelf. This species is one of the few whose remains were found in the inner-shelf region.

Water depths at which remains of individual fish species occurred ranged from 44 to 567 m. Considerable differences in depth range were evident among species, probably in part because of the sparse representation of some. Depth-of-occurrence data, by species, are summarized in Table 18 and Figure 22. Only two species, "*Stromateus*" and *Merluccius bilinearis*, were found at depths shallower than 50 m, and only six occurred at less than 100 m. On the other hand, 15 species were recovered from depths greater than 200 m, and 6 from depths greater than 360 m. The species that were distributed over the widest depth range are *Ceratoscopelus maderensis* and *Citharichthys ?arctifrons;* their remains were taken at depths from 95 to 567 m. Other species whose remains were spread over a wide depth range are: *Benthosema glaciale*, *Diaphus* sp.-2, *Diaphus* sp.-4, and *Lepophidium cervinum*. About 61% of the species were found

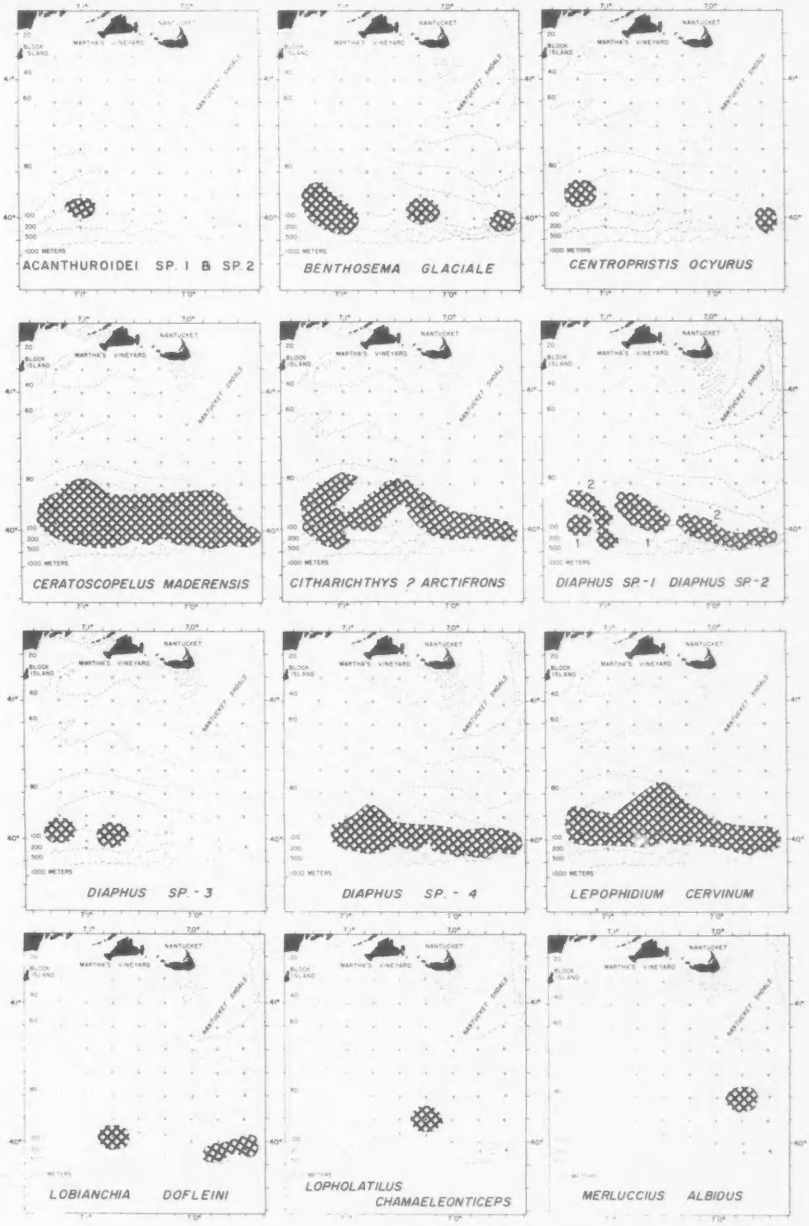

FIGURE 21.—Geographic distribution of fish otoliths, by species.

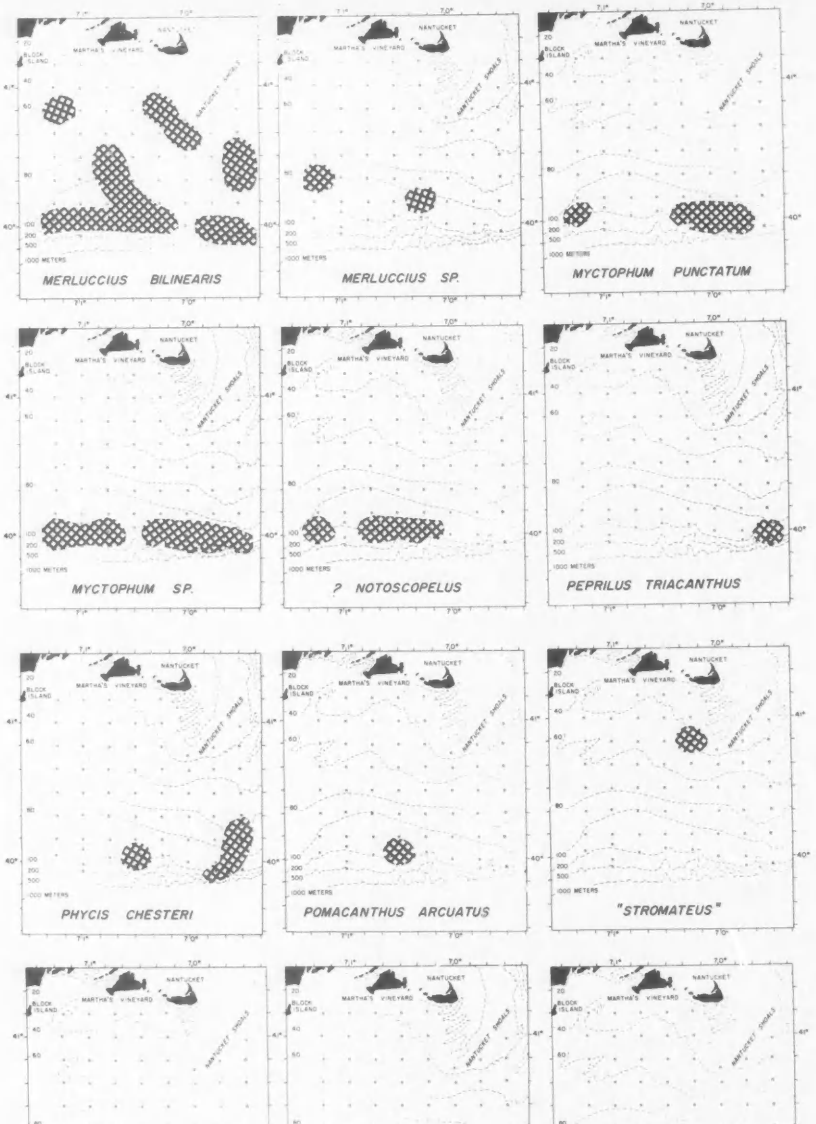

FIGURE 21.—Geographic distribution of fish otoliths, by species.—Continued.

TABLE 18.—Bathymetric distribution of teleost and selachian remains by species or higher taxon, and the number of stations at which each occurred. All entries are based on otoliths except *Prionace glauca*, which is represented by a tooth.

[P — pelagic, G — groundfish, and Un — unclassified.]

Species or higher taxon	Water depth			Number of stations	Environmental classification
	Minimum	Maximum	Mean		
	m	m	m		
Acanthuroidei sp.-1	179	179	179	1	G
Acanthuroidei sp.-2	179	179	179	1	G
Benthosema glaciale	183	567	296	5	P
Centropristis ocyurus	110	183	146	2	G
Ceratoscopelus maderensis	95	567	185	19	P
Citharichthys ?arctifrons	97	567	196	10	G
Diaphus sp.-1	132	220	176	3	P
Diaphus sp.-2	110	567	227	7	P
Diaphus sp.-3	183	194	188	2	P
Diaphus sp.-4	132	366	196	10	P
Lepophidium cervinum	97	366	169	17	G
Lobianchia dofleini	183	201	193	3	P
Lopholatilus chamaeleonticeps	113	113	113	1	G
Merluccius albidus	79	79	79	1	Un
Merluccius bilinearis	44	220	126	15	Un
Merluccius sp.	91	113	102	2	Un
Myctophum punctatum	139	201	174	5	P
Myctophum sp.	139	201	178	8	P
?Notoscopelus	183	220	195	4	P
Peprilus triacanthus	183	183	183	1	Un
Physcis chesteri	91	220	171	3	G
Pomacanthus arcuatus	220	220	220	1	G
Prionace glauca	179	179	179	1	Un
"*Stromateus*"	44	44	44	1	P
Urophycis chuss	113	194	163	3	G
Urophycis ?floridanus	113	113	113	1	G
Urophycis tenuis	183	201	189	3	G
Urophycis sp.	73	366	220	2	G

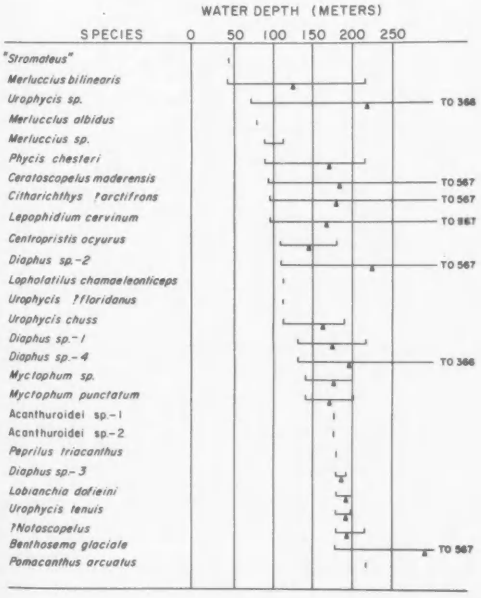

FIGURE 22.—Bathymetric range and mean depth of occurrence of fish species represented in the samples by otoliths. (Observed values are listed in Table 18.)

only in the general vicinity of the shelf break (100 to 220 m). None was restricted to a depth below 220 m.

REMAINS OF CRUSTACEANS AND COELENTERATES

Crustaceans and coelenterates were the least numerous of all taxonomic groups represented in the samples and formed only a small portion of the total macroscopic animal remains. These two groups differed markedly in geographic distribution, bathymetric distribution, and abundance. Thus, each is treated in a separate section below.

CRUSTACEANS

Remains of two groups of crustaceans—cirripedes and decapods—were present in the samples. Cirriped (barnacle) remains consisted of calcareous plates, primarily compartments (wall plates) plus a moderate proportion of opercular valves. Only balanomorph types were present, and generally the thicker, more durable portions were most numerous. Examples are illustrated in Figure 23. None of the chitinous parts of the skeleton, such as the covering of the appendages, was present. Decapod crustaceans were represented by anomuran (hermit) crabs and brachy-

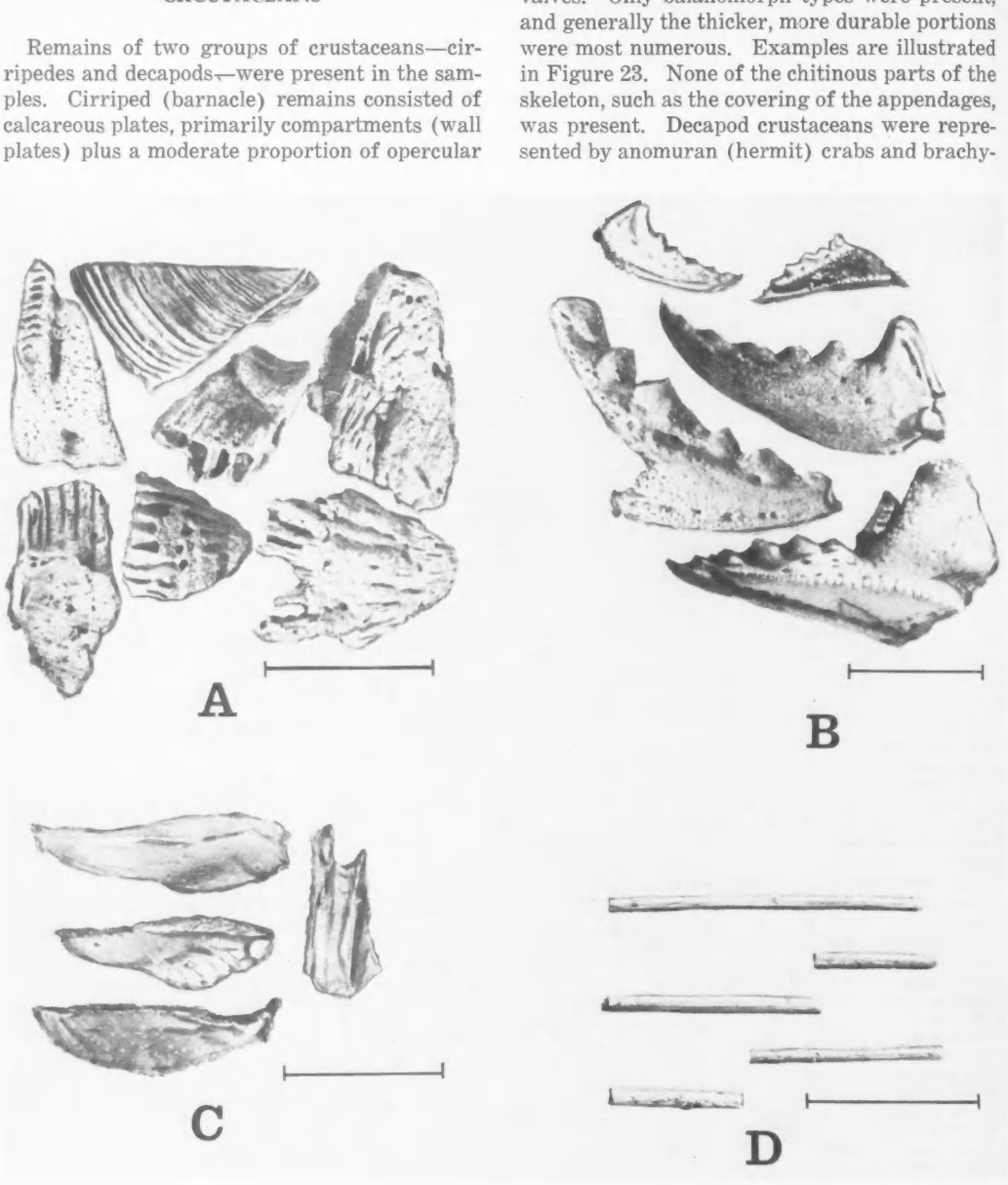

FIGURE 23.—Skeletal remains of crustaceans and coelenterates. A - cirripedes, scutum and compartments; B - anomuran and brachyuran, chelipod remains; C - *Flabellum*, corallite fragments; D - *Acanella* (?), axial skeleton remains. Each scale bar is 5 mm.

uran (true) crabs. Remains of the latter group consisted of the larger more massive and durable parts of the skeleton (mainly the carapace and chelipeds), and the anomuran remains consisted only of chelipeds. Occurrence records for both groups of crustaceans are included in Table 19; bathymetric data are given in Table 20. The geographic and bathymetric distributions are illustrated in Figures 24 and 25.

Remains of cirripedes (Figure 23A) were widely scattered over the area (Figure 24). The density of major fragments ranged from 10 to 90/m²; densities were substantially higher in shallow water than in deep water. The depth range was 27 to 567 m with the average depth at 123 m.

Remains of crustaceans carapaces and chelipeds were from anomuran and brachyuran crabs (Figure 23B). They were sparse to moderately dense and had a somewhat limited geographic distribution near the central part of the shelf (Figure 24) at depths from 51 to 113 m. Their distribution was much more restricted than that of cirripedes. Also, this part of the shelf is a low-energy region, as compared with the Nantucket Shoals and the shallow inshore areas where cirriped remains were prevalent.

TABLE 19.—Density of crustaceans and coelenterates, by station.

Station number	Crustaceans		Coelenterates	
	Cirripedes	Anomuran-brachyuran	*Flabellum*	*Acanella*(?)
	No/m²	*No*/m²	*No*/m²	*No*/m²
1	90	--	--	--
2	50	--	--	--
12	--	20	--	--
16	50	--	--	--
18	--	10	--	--
21	10	--	--	--
23	10	10	--	--
24	--	10	--	20
25	--	20	--	--
26	--	10	--	--
29	10	--	--	--
32	--	70	--	--
34	--	10	--	--
35	--	--	--	50
36	10	--	--	--
38	--	--	30	--
41	--	20	--	--
49	10	--	--	--
51	10	--	--	--
52	--	--	80	--
53	10	--	10	--
54	--	--	50	--
55	30	--	--	--
59	10	10	--	--
63	80	--	--	--

TABLE 20.—Bathymetric distribution of crustaceans and coelenterates, and the number of stations at which they occurred.

Group	Water depth			Number of stations
	Minimum	Maximum	Mean	
	m	m	m	
Crustaceans				
Cirripedes	27	567	123	13
Anomuran-brachyurans	51	113	76	10
Coelenterates				
Flabellum	146	366	221	4
Acanella (?)	90	97	94	2

COELENTERATES

Coelenterate remains were the rarest group of animals in the prefossil assemblage. They consisted solely of corals: *Flabellum alabastrum* (=*goodei* Verrill), a cup coral, and *Acanella* (?), a bush coral. Some examples of each kind are illustrated in Figure 23.

Flabellum, a solitary coral of the madreporian group, has a rather large (4 by 6 cm) polyp and a typical calcareous skeleton (corallite) with well-developed septae. Corallite remains contained a large proportion of septae and were commonly 4 to 8 mm long. This species occurred only in a limited area on the continental slope south of Martha's Vineyard (Figure 24) at depths of 146 to 366 m (Figure 25). Densities of fragments were as high as 80/m², but the average density at the locations where they occurred was about 40/m².

White calcareous rodlike structures about 0.5 mm in diameter and 0.5 to 1 cm in length (Figure 23D) were provisionally classified as *Acanella*, a colonial alcyonarian coral. The fragments appeared to be internodal portions of the axial skeletons. *Acanella normani* Verrill is not uncommon in the region. The multibranched colony of this species is composed of numerous slender, jointed segments. Total height of a full-grown colony is usually less than 30 cm. Remains of this coral were found at two stations near the center of the area (Figure 24) at depths of 90 to 97 m and in densities of 20 to 50/m².

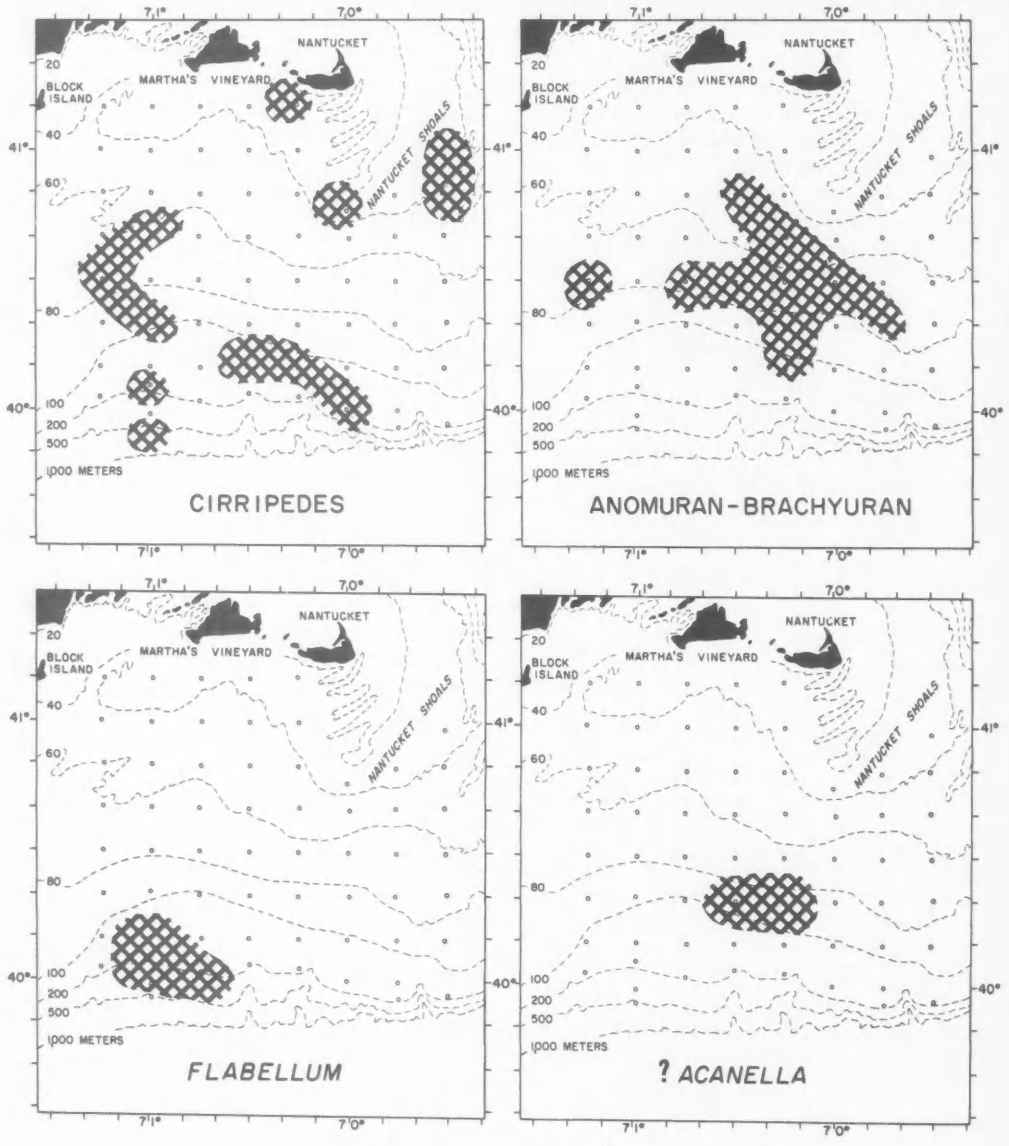

FIGURE 24.—Geographic distribution of skeletal remains of crustaceans and coelenterates.

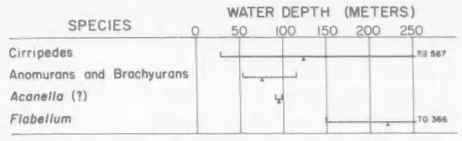

FIGURE 25.—Bathymetric distribution of skeletal remains of crustaceans and coelenterates.

COMPARATIVE DISTRIBUTION OF ALL TAXONOMIC GROUPS

The distribution of the principal animal remains in relation to each other, sediment type, and water depth, and, to a limited extent, their north-south geographical position on the continental shelf and slope are illustrated in Figure 26. This chart is a generalized profile of the study area with the inshore (north) section on the lefthand side and the offshore (south) section on the righthand side. Broad, diagonally striped bands indicate relatively high density, and narrow lines indicate low density. Animal groups whose centers of concentration were inshore in relatively shallow waters were cirripedes and *Echinarachnius parma*. The dominant midshelf and outer-shelf components were gastropods, pelecypods, and decapods. Pelecypods, scaphopods, *Brisaster*, and *Flabellum* were common along the outer portion of the continental shelf and upper portion of the continental slope. The chief components in deeper sections of the continental slope were fish otoliths and cephalopod mandibles.

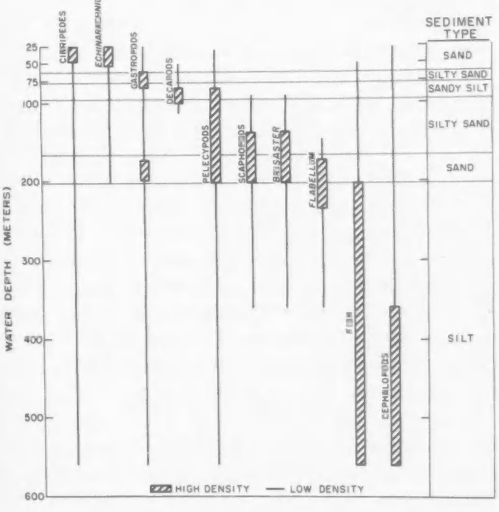

FIGURE 26.—Schematic diagram of the density distribution of macroscopic remains of the major animal groups represented in bottom sediments arranged according to water depth and sediment type (see text for details).

SUMMARY

Skeletal remains of deceased animals were common seabed components on the southern New England continental shelf and the upper part of the continental slope. In some sections, particularly in shallow water, skeletal remains constituted a substantial portion of the substrate volume—up to nearly 30% in the vicinity of Nantucket Shoals. Offshore, near the margin of the continental shelf and in the upper portion of the continental slope, macroscopic animal remains generally constituted less than 1% of the substrate.

Remains of benthic, pelagic, and nektonic organisms were present; benthic forms were dominant. Planktonic animals (represented only by pteropods) were sparse. Fish and cephalopods were the principal nektonic forms. They were rather abundant in the deeper waters, particularly on the outer portion of the continental shelf and on the continental slope.

The two animal groups that contributed the largest quantities of material to the substrate were echinoid echinoderms and pelecypod mollusks. Although remains of a wide variety of fish species were present, the quantity was moderate and the sizes small; consequently the volume of fish remains was rather small.

ECHINODERMS

The exceedingly abundant remains of echinoderms consisted exclusively of echinoids. Only one species—*Echinarachnius parma*—occurred in high densities and was the most abundant and widely distributed component of organic

origin in the sediments. Geographically it had a wide distribution, occurring at 72% of the stations. Depth range was 27 to 201 m. Size, shape, and color of *Echinarachnius* fragments differed markedly with water depth and sediment type. The *E. parma* fragments in the inshore localities were whitish, relatively large, and had angular edges and corners; in offshore localities, the fragments were light greenish-brown, smaller, and had rounded edges. Densities of echinoids other than *Echinarachnius* were low, and except for *Brisaster*, remains were found at only a few localities. Density of *Brisaster* remains were low but the remains were rather widely distributed along the outer portion of the continental shelf. Remains of *Strongylocentrotus drobachiensis* were sparse and widely scattered in both shallow and deep water.

MOLLUSKS

Pelecypods ranked first in diversity of forms (57 species) and second in volume of remains in the bottom sediments. They were present at all depths sampled, from 27 to 567 m, and were widely distributed geographically. Densities were high in a wide band extending from Nantucket Shoals southwestward across the area, and in a narrow band parallel to the isobaths near the shelf break. Pelecypods were very abundant (more than 3,000/m^2) at 6 stations, most of which were along the outer margin of the continental shelf; common to abundant (50 to 3,000/m^2) at 48 stations; and sparse (less than 50/m^2) or absent at 8 stations. In general, the species with the broadest geographic distributions occurred in highest densities. The six most abundant and widely distributed pelecypods were: *Venericardia borealis, Arctica islandica, Astarte subequilatera, A. undata, Nucula proxima,* and *Thyasira trisinuata.* Pelecypod shells were more abundant in moderately fine-textured sediments than in either the coarse or very fine sediments. Silty sand, sandy silt, and sand-silt-clay yielded the highest densities of pelecypod shells. Size of shells ranged from 10 to 12 cm (*Spisula, Arctica, Placopecten*) to less than 5 mm (*Thyasira, Nucula, Bathyarca*).

Gastropods ranked third in volume of skeletal material in the substrates. Shells of gastropods were distributed widely throughout the area, but highest densities were near the center. A total of 44 species were present, but only 2 were generally abundant—*Alvania carinata* and *Cylichna gouldi.* Shells were taken at all depths, and were particularly common between 60 and 80 m and moderately common between 175 and 250 m. Density was correlated in a general way with bottom sediments. High densities were in silty sand and sand sediments, whereas shells were absent in coarse sand and mixtures of sand and gravel. A large majority of gastropod shells was less than 1 cm in height.

Cephalopod remains, consisting entirely of beaks, were present at only 12 stations, all of which were from the outer portion of the continental shelf and upper part of the continental slope at depths between 76 and 567 m. Densities were generally less than 40/m^2 at the shallower depths, but ranged to 130/m^2 at a depth of 366 m and 11/m^2 at 567 m. Remains of this group ranged in size from 4 to 6 mm and were relatively fragile. They were recovered only from fine-textured sediments.

Distributions of scaphopods were rather limited geographically and densities were low. The two genera collected, *Cadulus* and *Dentalum,* were present at 11 stations, geographically limited to the deepwater areas on the outer portion of the continental shelf and the upper continental slope. The bathymetric range was 139 to 366 m for *Cadulus,* and 91 to 183 m for *Dentalium.* Sediments at the scaphopod localities were generally fine-grained, but *Cadulus* occurred in slightly coarser sediments than *Dentalium.* Densities at the stations where they occurred averaged about 30 to 40/m^2; maximum density for both genera was 11/m^2. *Cadulus* shells were 10 to 13 mm long, and *Dentalium* shells were 15 to 35 mm.

FISH

Fish were the only vertebrates in the samples. Otoliths were the main component and bones were moderately common, but teeth and scales were rare. Remains of 26 species were collected, nearly half of which were from epipelagic or mesopelagic forms. Myctophids were the most numerous and widely distributed, and they con-

tributed the greatest number of species. Thirty-six percent of the species and 87% of all otoliths were Myctophiformes. The six most abundant fish, based on otolith identifications, were: *Ceratoscopelus maderensis*, *Citharichthys ?arctifrons*, *Diaphus* sp.-4, *Lepophidium cervinum*, *Merluccius bilinearis*, and *Myctophum* sp. The estimated length of the fish whose remains were encountered ranged from a few centimeters to several meters. Remains of fish were at depths between 38 and 567 m, and an overwhelming majority was found at depths greater than 150 m. More than 90% of the otoliths were at depths below the 150-m isobath; bones were less common and more uniformly distributed, from 38 to 366 m. The remarkably high otolith density of 3,030/m² was found near the edge of the continental shelf south of Nantucket Shoals. Remains of most individual species were geographically distributed in east-west bands across the area, generally oriented parallel to the isobaths. Fish remains were absent in coarse-grained sediments, and most abundant in fine sands and silt-clay.

CRUSTACEANS AND COELENTERATES

Crustaceans and coelenterates were the only other nonmolluscan invertebrates, in addition to those previously described, that were present in the samples. The quantity of their remains was very small.

Crustaceans were generally sparse and rather widely distributed. Cirripedes consisted exclusively of shells of sessile forms; they were geographically scattered and were taken at all depths sampled. Cirripedes were only slightly more common in shallow water than in deep water. They were one of the few animal groups whose remains occurred in coarse-grained sediments. Fragments of skeletons of anomurans and brachyurans were encountered only in the midcontinental shelf in sediments primarily of silts and fine sands. They were collected between 51 and 113 m. Densities were low, from 10 to 70/m².

Remains of coelenterates occurred in low densities (10 to 80/m²) and were geographically restricted to small areas in the south-central and southwestern sectors. Two genera—both corals—were represented, *Acanella* (?) (at 90 to 97 m) and *Flabellum* (between 146 and 366 m). Both kinds were restricted to fine-textured sediments.

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DEEP MAXIMA OF PHOTOSYNTHETIC CHLOROPHYLL IN THE PACIFIC OCEAN

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ABSTRACT

Data collected on several expeditions through the temperate and tropical Pacific Ocean show that during most of the year the maximum concentrations of chlorophyll occur below the surface, typically in a narrow layer near or below the depth of penetration of 1% of the surface light. The layer appears to be continuous across most of the Pacific although the depth and chlorophyll concentration vary regionally. The depth of the layer is more closely related to the depth of the nitrite maximum and to the position of the nutricline than to either light or density regimes. Productivity within the layer is low but positive, and contributes substantially to the total production of the water column. The maximum layer may be a seasonal phenomenon developing in the summer after the stabilization of the water column and mixing to the surface during the winter. Year to year fluctuations of depth and concentration of chlorophyll within the maximum layer may be related to large-scale meteorological fluctuations.

Doty and Capurro (1961) have tabulated the position, date, depth, and values of chlorophyll and productivity in the world's oceans. There are several thousands of these measurements in the Pacific. Most are in the Northern Hemisphere, and most are near land masses or islands (e.g., Hawaii, Luzon, Hokkaido, New Caledonia, New Zealand), along the equator, or north of lat 40°N. Of the values from the oceanic Pacific, between lat 50°N and 50°S, less than 10% of the chlorophyll values represent depths greater than 25 m; in the same region, over half of the productivity measurements were obtained at the sea surface. Koblenz-Mishke, Volkovinsky, and Kabanova (1970) have used these data and additional data available to them to estimate the plankton primary production of the Pacific, to construct tables and charts of its geographical variability, and to compare production in the Pacific with their estimates from other oceans. Their estimates of primary production, expressed in milligrams carbon per square meter of sea surface per day, represent production integrated through the water column. However, many of their production values are extrapolated from surface measurements, and, in large areas of the temperate gyres of the North and South Pacific, production is estimated from the available chlorophyll data, or from "oxygen or hydrogen saturation" values.

All values of total production in the water column are strongly dependent upon the assumed (usually) depth of zero productivity. This is traditionally taken to be the depth at which the light intensity has been reduced to 1% of the incident radiation, and this criterion has been used to divide the water column into a euphotic zone and an aphotic zone.

Evidence is accumulating that major concentrations of plant material in the ocean usually occur below the surface, typically within the thermocline and near the bottom of the euphotic zone. Maxima of chlorophyll or phytoplankton as deep as 100 m have been reported from the Indian Ocean (Yentsch, 1965), the Sargasso Sea (Menzel and Ryther, 1960), the Gulf of Mexico (Steele, 1964), and the Kuroshio and adjacent regions (Motoda and Marumo, 1963; Saijo, Iizuka, and Asaoka, 1969). Shallower maxima are characteristic of the California Current

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(Allen, 1939; Lorenzen, 1965, 1967). Initial results of the EASTROPAC survey (Love, 1970, 1971) indicate a chlorophyll maximum varying in depth between 50 and 100 m over large areas of the eastern tropical Pacific. Anderson (1969) has studied the chlorophyll maximum layer off the Oregon coast which is present between 50 and 75 m during the summer. The layer is continuous over a broad region in the Eastern Subarctic Pacific and maybe transpacific. Chlorophyll maxima have also been reported from the other major water masses of the Pacific (El-Sayed, 1970; Sorokin, 1970).

Different workers have attributed the existence of the maximum layer to different processes including the concentration of detrital chlorophyll in the pycnocline (Lorenzen, 1965), differential zooplankton grazing (Lorenzen, 1967), an increase in the chlorophyll/carbon ratio in plant cells, without an accumulation of cells (Steele, 1964), horizontal advection and layering of different water masses and plant populations (Sano, 1966), the sinking of active or senescent cells from shallower depth (Allen, 1932; Steele and Yentsch, 1960), and in situ production (Anderson, 1969). In short, the tendency has been to consider deep chlorophyll maximum layers as discrete and sporadic phenomena and to interpret them strictly according to local conditions.

The accuracy with which surface productivity reflects the productivity throughout the water column has been investigated by Koblenz-Mishke et al. (1970) by means of log-log scatter diagrams. There is a linear trend in their transformed data, but the spread of values around the regression line is broad. Lorenzen (1970) showed a significant linear regression, after transformation to logarithms, of total production on the concentration of surface chlorophyll. The regression, however, removes only half of the variability of the dependent variable, and the author advises that precise values of total production must depend upon direct measurements. He also cautions that extrapolations from surface values are based upon averages and will easily miss unexpected events.

There have been very few attempts to measure productivity in the deeper maximum layers. Anderson (1969) made one series of in situ measurements within the chlorophyll maximum layer off the Oregon coast. There was a peak in production within the layer and positive photosynthesis as deep as 90 m, the 0.1% light level. Implicit in most studies to date is the assumption that pigment concentrations below the level of 1% light are nonphotosynthetic and represent a loss of plant material from the "euphotic zone." The two extensive surveys from the Sargasso Sea and the eastern tropical Pacific both adjusted the depth of the lowest sample to the depth of 1% light, and rarely sampled below 100 m, even though the maximum pigment concentrations were frequently obtained from the deepest sample.

In the present paper, the authors have summarized a large amount of data accumulated over the past 8 years, all of which indicate that a deep chlorophyll maximum layer is a regular and continuous feature of much of the oceanic Pacific. It is frequently observed below the traditionally defined euphotic zone, yet it is dominated by photosynthetically active chlorophyll *a* which is present in concentrations as great as 10 times those at the surface. The development of this maximum layer appears not to be a localized process, but a widespread and regularly occurring phenomenon. Because of its limited vertical extent and great depth, the existence, extent and significance of this maximum layer has been overlooked by most previous surveys of chlorophyll and productivity. Evidence suggests that a better understanding of this layer will necessitate revision of existing estimates of total primary production in the ocean.

METHODS

Since 1964 we have been mapping and studying the subsurface chlorophyll maximum in the Pacific on a series of expeditions (Figure 1). In 1964 (URSA MAJOR Expedition: University of California, 1967) and 1966 (ZETES Expedition: University of California, 1970), chlorophyll pigments were determined with a D U Spectrophotometer; on other expeditions chlorophyll *a* and phaeophytin were assayed with a

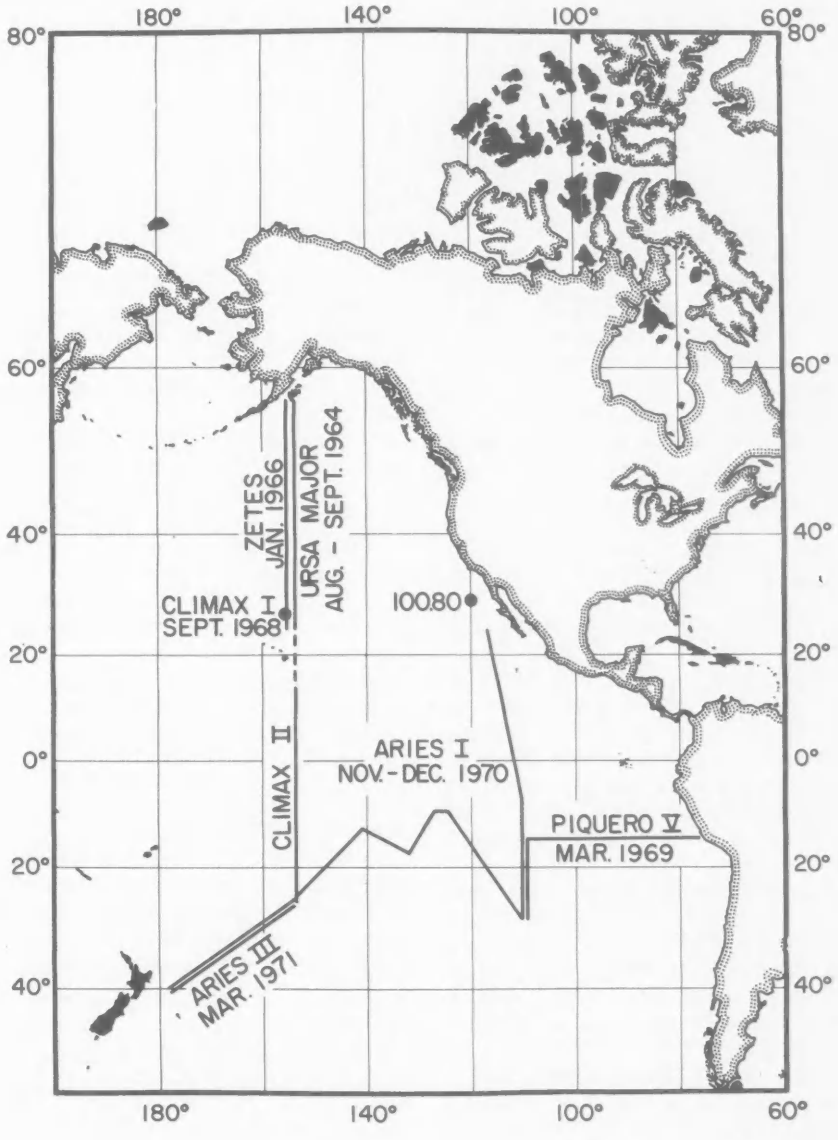

FIGURE 1.—Cruise tracks of seven expeditions from which chlorophyll data was obtained, and the location of Marine Life Research station 100.80 at which chlorophyll was sampled seasonally.

Turner Fluorometer.[2] Water samples from the same casts were preserved with neutral Formalin for subsequent phytoplankton enumeration. Additional measurements have routinely included temperature and salinity, determined with an STD; oxygen, determined by the Winkler procedure; and phosphate, silicate, nitrate, and nitrite, measured with the spectrophotometer or the autoanalyzer (Strickland and Parsons, 1968). On CLIMAX II and ARIES III ammonia was assayed (Solórzano, 1968). On stations occupied at noon, the transparency of the water was measured with a secchi disk and the compensation depth was estimated by multiplying the terminal depth by three. A wide variety of zooplankton samples were collected on all expeditions.

On the expeditions CLIMAX I, CLIMAX II, and ARIES III, observations were concentrated in two areas of the North and South Pacific, near the axes of the Central Pacific Gyres. In these regions, in addition to the above measurements, productivity was routinely measured by the uptake of C-14 by samples incubated on deck in simulated in situ incubators (Owen and Zeitzschel, 1970) and less frequently by samples incubated in situ (Steeman Nielsen, 1952). Penetration of light into the ocean was measured with a submarine photometer (Austin and Loudermilk, 1968). Coincident secchi disk determinations tended to overestimate the depth of 1% light, though the agreement was usually within 6 m. A submersible pump with a deck mounted filtering system was used to obtain stratified samples for determination of biomass (dry weight) of three size categories of zooplankton (333 μ and greater, 332-103 μ, and 102-35 μ). The same pump supplied water to the fluorometer, equipped with a flow-through door, and to the autoanalyzer for continuous vertical profiles of chlorophyll and nutrients (Beers, Stewart, and Strickland, 1967).

In September 1968 (CLIMAX I Expedition), a pair of parachute drogues, set at 10 m depth, were released at lat 27°N, long 155°W, and followed for 10 days, during which time they moved northwest approximately 150 miles. Physical, chemical, and biological properties were sampled continuously on a 24-hr schedule. In September-October 1969 (CLIMAX II Expedition), a grid of ten 24-hr stations was occupied along long 155°W between lat 27°10′ and 28°30′N, and a grid of six 24-hr stations was occupied along the same meridian between lat 24°40′ and 25°20′S. This latter pattern was repeated in March 1971 (ARIES III Expedition). The sampling routine was similar on each of these expeditions. Each 24-hr station included four casts for nutrients and chlorophyll, day and night samples for biomass of micro- and macrozooplankton, and a simulated in situ productivity experiment. In 1969 and 1971 a single in situ productivity experiment followed the routine station plan.

In addition to data collected on S.I.O. (Scripps Institution of Oceanography) expeditions, we have available data from the California Current collected by institutions participating in the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program. We have made use of data from station 100.80 which is located near the western edge of the California Current.

GEOGRAPHICAL DISTRIBUTION

Chlorophyll data collected on several expeditions have been combined and contoured in Figure 2. It is clear from these that a subsurface layer of high chlorophyll concentration is present across vast areas of the Pacific Ocean during many months of the year. South of lat 46°N, the maximum concentrations of chlorophyll are frequently observed at greater depths than the estimated 1% light level. The depth of the maximum along the meridianal transects shows no relationship with either temperature, salinity, or density.

The chlorophyll maximum layer shoals near land, and in regions of general upwelling such as the North Subarctic Gyre and the Equatorial belt. It deepens near the axes of the Central Pacific Gyres. The meridianal continuity of the layer is especially remarkable considering that it passes through three major epipelagic environments: the Subarctic, where it is likely to

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

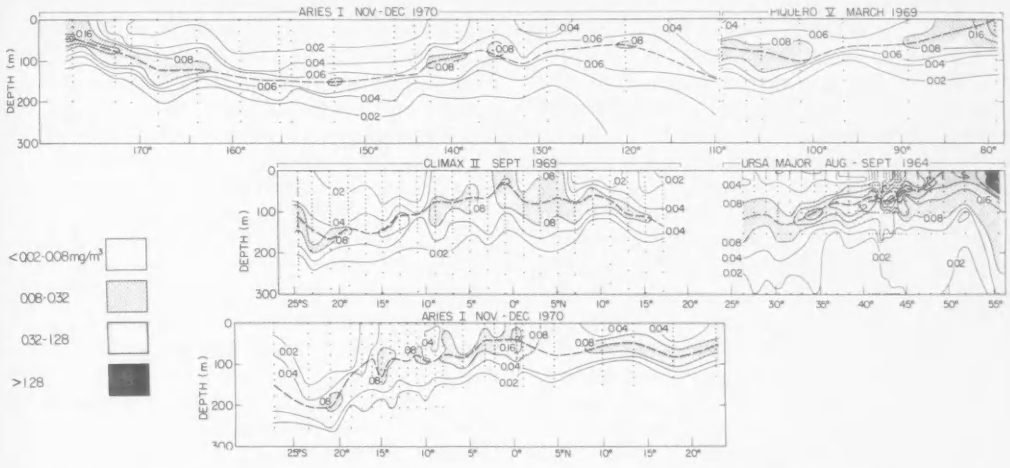

FIGURE 2.—Vertical sections of chlorophyll *a* concentrations in the Pacific Ocean; vertical exaggeration 5020.

be confluent with that discussed by Anderson (1969), the Central, and the Equatorial environments.

The east-west section indicates that the maximum layer is well developed over most of the middle latitudes of the South Pacific. The maximum layer in the South Central Gyre tends to be deeper, and the chlorophyll concentrations throughout the water column tend to be lower than in corresponding areas of the North Pacific. The greatest depth so far observed by us was at lat 20°09′S, long 118°18′W, during December (ARIES I Expedition) where a layer containing 0.05 mg/m³ occurred between 200 and 245 m depth; chlorophyll values at the surface were less than 0.01 mg/m³.

Portions of all three sections have been repeated by different expeditions. The depth and concentration of chlorophyll in the maximum layer vary somewhat, but the general features remain the same. In 1969, the Ocean Research Institute, University of Tokyo, ran a transect along long 155°W (Ocean Research Institute, University of Tokyo, 1970). The results of their chlorophyll measurements compare well with ours.

VERTICAL DISTRIBUTION

We have supplemented our discrete, quantitative chlorophyll samples with in vivo profiles of fluorescence which provide continuous, but qualitative pictures of the fine scale structure of the maximum layer (Figure 3). Although the major

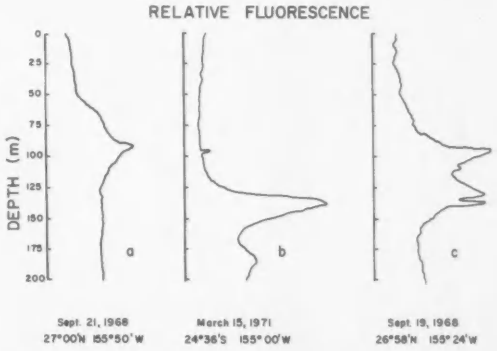

FIGURE 3.—Continuous vertical profiles of in vivo fluorescence of chlorophyll. a) a simple maximum layer in the North Central Pacific; surface chlorophyll concentration 0.02 mg/m³; b) a simple maximum layer in the South Central Pacific; surface chlorophyll concentration 0.01 mg/m³; c) a double maximum layer in the North Central Pacific; surface chlorophyll concentration 0.02 mg/m³.

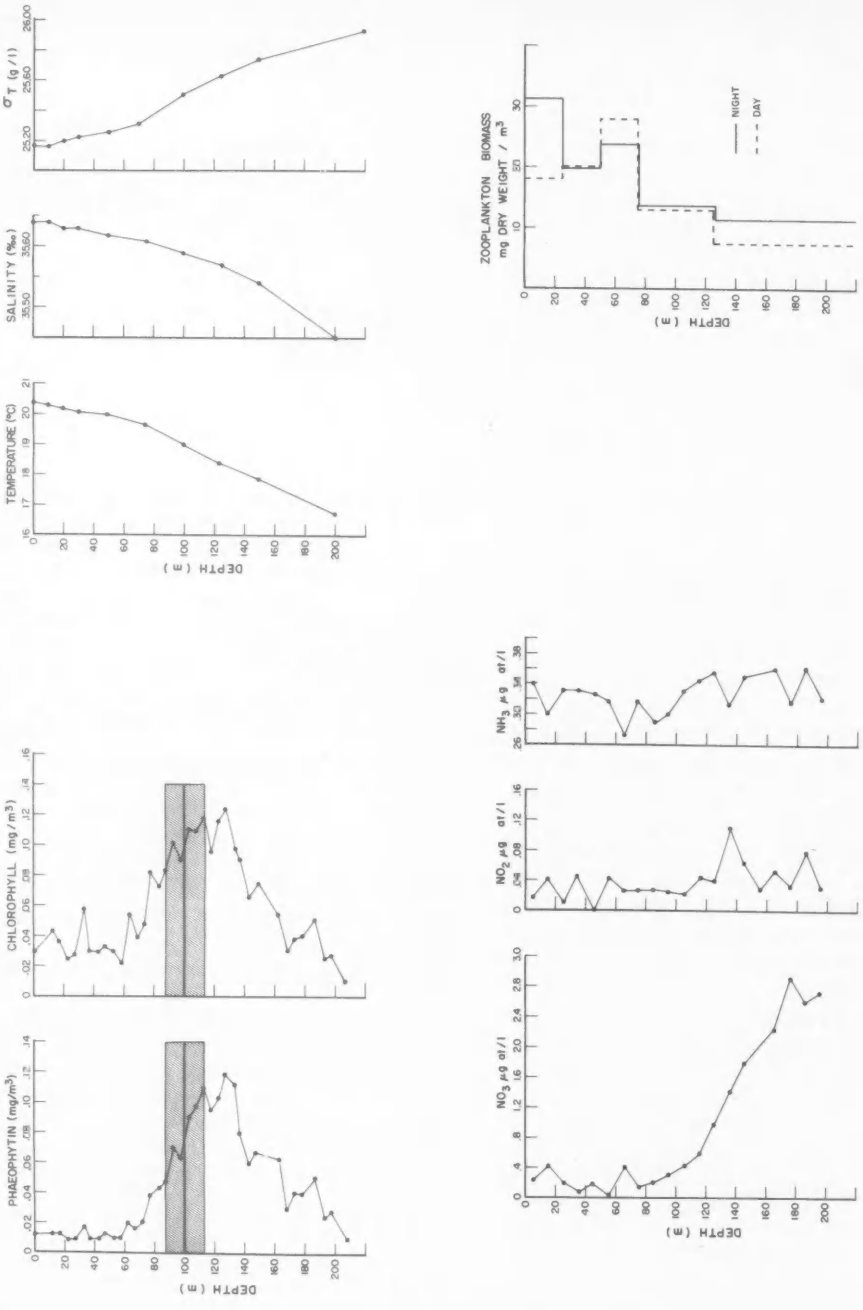

FIGURE 4.—Vertical profiles of chlorophyll, phaeophytin, and other physical, chemical, and biological properties observed in October 1969 in the vicinity of lat 25°S, long 155°W. Estimated depth of the 1% light level and 95% confidence interval indicated by horizontal bar and cross hatching.

accumulation of pigment generally occupies a layer 50-75 m thick, the core of the layer may be very abrupt. From closely spaced water samples (Table 1) we have found that the highest concentrations of chlorophyll may be contained in a layer less than 5 m thick and may exceed by 10% to 50% the concentrations in the adjacent samples. Occasionally maximum concentrations are found in more than one layer within the region of chlorophyll accumulation (Figure 3c, Table 1, 23 August 1967).

It is very difficult to sample such a narrow core with discrete water samplers. A routine cast, in which samples are usually spaced at least 15 m apart, is likely to miss the peak concentrations, and underestimate the chlorophyll content of the maximum layer. Moreover, because of the rapid vertical changes in chlorophyll concentration, slight variations in the position of the samples within the layer may appear as horizontal discontinuities of the layer. Discrete chlorophyll data, including those presented in this paper, must be interpreted accordingly.

SPECIES COMPOSITION

The numbers and species of diatoms in water samples collected on expeditions URSA MAJOR and ZETES have been enumerated (University of California, 1967, 1970; Venrick, 1969). The increase in chlorophyll concentration in the maximum layer is accompanied by a significant increase in the number of diatom cells. Furthermore, the maximum layer is composed of different assemblages of species within the Subarctic Pacific, the Transition Domain, and the Central Pacific (Venrick, 1971). In August, north of lat 40°N the species within the maximum layer were the same as those occupying the overlying water mass. South of lat 38°N, however, samples from the maximum layer were dominated by species which were not observed in shallower samples. During the winter when the maximum layer had been eroded by increased turbulence, the same species were present, but they were distributed randomly through the water column.

More recent studies were undertaken in 1968 at lat 26°57′N, long 155°10′W with a series of 19 replicate casts over a distance of 10.5 miles. Phytoplankton samples were collected from 25 m, 50 m, 75 m, and from the chlorophyll maximum layer at 125 m. A total of 80 species of diatoms were identified, of which 24, 36, and 37 were observed in the samples collected from 25 m, 50 m, and 75 m, respectively. A total of 64 spe-

TABLE 1.—Fine scale structure of the chlorophyll maximum layer.

URSA MAJOR		CLIMAX II			
2 Sept. 1964 lat 43°49′N, long 154°44′W		26 Aug. 1969 lat 27°09′N, long 155°18′W		23 Aug. 1969 lat 28°29′N, long 155°16′W	
Depth (m)	Chlorophyll *a* (mg/m³)	Depth (m)	Chlorophyll *a* (mg/m³)	Depth (m)	Chlorophyll *a* (mg/m³)
0	0.10	1	0.06	0	0.06
20	0.11	20	0.06	20	0.06
50	0.55	39	0.07	40	0.06
60	1.19	58	0.06	60	0.06
65	0.94	77	0.06	80	0.06
70	0.73	96	0.08	90	0.08
75	0.56	101	0.07	100	0.13
80	0.44	105	0.11	105	0.13
85	0.38	110	0.08	110	0.09
90	0.24	114	0.08	114	0.13
100	0.10	124	0.06	118	0.12
		141	0.02	122	0.10
				126	0.07
				130	0.07
				135	0.06
				140	0.04
				150	0.04
				165	0.03
				180	0.02
				200	0.02

cies were found at 125 m, and of these 64, 22 occurred only in samples from that depth. Thus, the chlorophyll maximum layer, which has a higher species diversity (as measured by the number of diatom species) and which may contain species not found at shallower depths appears to offer unique features as a biological habitat.

THE CENTRAL PACIFIC

Studies conducted on Expeditions CLIMAX I, CLIMAX II, and ARIES III near the axes of the North and South Central Pacific Gyres have provided us with a large amount of data concerning the vertical distribution of chlorophyll and productivity in the water column and their relationship with other physical, chemical, and biological parameters. Comparison with data collected over much wider areas on other expeditions leads us to believe that the relations observed in the Central Gyres may be pertinent to much of the oceanic Pacic.

The vertical distribution of chlorophyll and net production observed during these four studies have been summarized in Table 2. All studies show a well-defined subsurface accumulation of chlorophyll which varies in width from 50 to 75 m and contains maximum concentrations of chlorophyll in excess of 0.10 mg/m³. The core of the layer always occurred below the depth penetrated by 1% of the surface radiation. In fact, more than half of the total chlorophyll within the water column was observed below this depth.

The rate of production per unit chlorophyll decreases with depth from a maximum at about 20 m, but this is partially offset by the increase in the amount of chlorophyll, and production rates as high as 0.13 mg C/m³/hr have been observed in the maximum layer in the South Pacific. Our in situ experiments indicate that 7% to 20% of the total production in the water column occurs below the 1% light level. These are minimum values since our in situ studies did not reach the level of no productivity. The total rate of production throughout the water column is variable on rather small spatial and temporal scales, but appears to be considerably greater than maximum estimate of 100 mg C/m²/day (8.3 mg C/m²/hr) estimated by Koblentz-Mishke et al. (1970).

The vertical distribution of chlorophyll and several relevant properties are illustrated in Figure 4. Data points are mean values of observations made in replicate on six 24-hr stations in the South Central Pacific (CLIMAX II Expedition) and represent an area of 60 square miles and a time span of 6 days. Above 200 m there was an average of 12.35 mg chlorophyll per square meter sea surface. Of this, over half occurred below the estimated depth of 1% light. We estimated the light intensity at the core of the maximum layer to lie between 0.10% and 0.26% of incident radiation. The vertical distribution of phaeophytin is similar to that of chlorophyll.

The accumulation of both chlorophyll and phaeophytin occurs within the pycnocline. On a local scale, these layers may move up and down with the pycnocline, for instance in response to

TABLE 2.—Mean value and 95% confidence limits of the mean for data relative to the vertical distribution of light, chlorophyll *a*, and productivity at two stations in the North and South Central Pacific Ocean.

Position	Date	Depth of 1% light m (1)	Chlorophyll *a*					Productivity	
			Depth of maximum m (2)	Surface concentration mg/m³ (3)	Concentration at (2) mg/m³ (4)	Water column total 0-200 m mg/m² (5)	% of (5) below (1) %	Total above (1) mg C/m²/hr	Total below (1) mg C/m²/hr
Lat 27°N, long 155°W	Sept. 1968	79 ± 5	104 ± 8	0.03 ± 0.01	0.16 ± 0.03	11.92 ± 2.62	73.5 ± 8.3	16.26 ± 2.25	
	Sept. 1969	73 ± 5	111 ± 9	0.09 ± 0.03	0.11 ± 0.02	11.67 ± 1.32	53.7 ± 4.6	31.74 ± 7.35	> 2.28
Lat 25°S, long 155°W	Oct. 1969	100 ± 13	122 ± 11	0.03 ± 0.01	0.13 ± 0.02	12.35 ± 3.22	58.5 ± 6.4	12.87 ± 9.08	> 3.28
	Mar. 1971	132 ± 14	140 ± 9	0.01 ± 0.00	0.11 ± 0.05	8.13 ± 1.47	58.3 ± 9.5	11.80	> 1.20

internal waves. However, on a wider scale, there appears to be no relationship between the depth of the maximum layer and any one isoline of temperature, salinity, or density.

Plant nutrients are present in very low concentrations in the upper 100 m. Phosphate values were less than 1.5 μg at./liter in the North Central Pacific and less than 0.2 μg at./liter in the South Central Pacific. Nitrate was less than 0.6 μg at./liter in the North and less than 0.8 μg at./liter in the South, while corresponding values of silicate ranged between 1 and 7 μg at./liter in the North and between 0 and 3 μg at./liter in the South. The concentrations of these three nutrients increase systematically and significantly at, or just below, the level of the chlorophyll maximum. Concentrations of ammonia are low and irregular throughout the upper 200 m, showing no pattern with depth. In contrast, high values of nitrite in the upper 200 m (occasionally as high as 4.5 μg at./liter) were observed only within or just below the chlorophyll maximum, and may indicate recent phytoplankton assimilation of nitrate-nitrogen (Vaccaro and Ryther, 1959). In all of our studies, the relationship between the vertical distributions of chlorophyll and nutrients was far more predictable than the relationship between chlorophyll and any of the physical properties.

We have found no evidence of any accumulation of zooplankton within the chlorophyll maximum layer. Total zooplankton biomass (animals greater than 35 μ) was greatest above the maximum layer during both day and night. This appears to be true for all size categories.

THE SEASONAL CYCLE

Seasonal samples from the western edge of the California Current (station 100.80 at lat 30°00′N, long 120°07′W) during 1969 demonstrate a seasonal change in the vertical distribution of chlorophyll *a* (Figure 5). We have evidence that this maximum layer is continuous with that observed within the Central Pacific Gyre and we expect their seasonal cycles to be comparable. For a short period in February, chlorophyll is essentially homogeneous through the upper 50 m. This corresponds in time to the maximum development of the mixed layer. When the water column begins to stratify in March, chlorophyll concentrations at the surface decrease abruptly and a subsurface maximum layer develops. As the summer progresses, the maximum decreases in concentration and the layer subsidies, reaching its maximum depth just prior to the breakdown of the density stratification in December. Figure 5b illustrates the lack of temporal relationship between the depth of the chlorophyll maximum and any one isopleth of density. This would seem to preclude the formation of the maximum layer from the accumulation of cells regulated solely by their physical density.

The vertical distribution of chlorophyll during August along long 155°W is presented in Figure 2. This may be compared with the

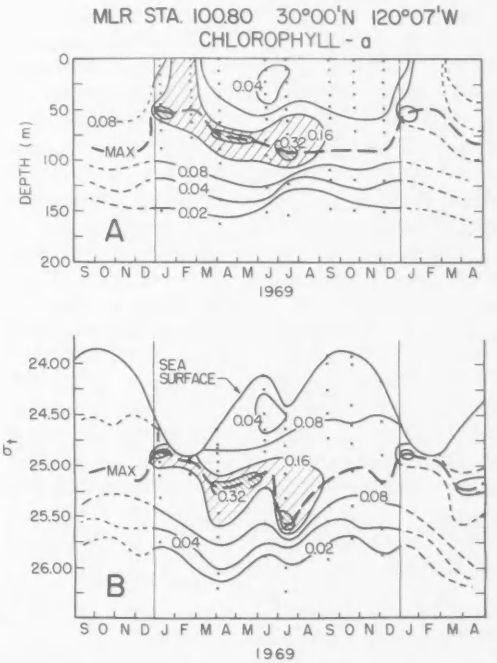

FIGURE 5.—Annual development of the subsurface chlorophyll maximum layer at lat 30°00′N, long 120°07′W. Chlorophyll *a* concentration is contoured with respect to depth (A) and density (B).

distribution along the same transect observed during January (ZETES Expedition) when a similar program of chlorophyll measurement was carried out. In January, north of lat 32°N, the mixed layer extends below 100 m. Concentrations of chlorophyll are uniform throughout this layer, decreasing abruptly below the mixed layer. Between lat 26°N and 32°N a weak chlorophyll maximum is still present near 120 m below the mixed layer which does not reach its greatest depth of 200 m until February (Robinson, 1951).

The evidence accumulated to date suggests that a subsurface concentration of plant material can persist only in the presence of a density gradient which isolates the layer from the effects of wind-driven turbulence. Thus, any seasonal fluctuations in the strength or depth of the pycnocline may be expected to affect the presence of the deep maximum layer. We can postulate with some assurance that in any environment in which the winter mixed layer regularly exceeds the depth of the chlorophyll maximum layer, the maximum layer must be a seasonal phenomenon. At any locality, the duration of the maximum layer will be determined by the duration of seasonal stratification of the water column and thus will be progressively shorter at higher latitudes.

This observation has important implications. Over most, if not all, of the ocean, the phytoplankton within the maximum layer do not represent a permanent loss to the epipelagic community. Neither need there be a balanced energy budget within the maximum layer. Sufficient energy may be produced and stored in a brief period prior to stratification of the water column or the depletion of nutrients from the surface waters to maintain the population within the maximum layer for considerable periods of time, even though photosynthesis may be depressed or absent.

LARGE-SCALE TEMPORAL FLUCTUATIONS

In the Central Gyre of the North Pacific we have recorded temporal fluctuations on a larger scale. In September 1969, the standing crop and productivity were higher and more variable throughout the water column than in the same month of the previous year. As a result, in 1969, the chlorophyll maximum layer was less sharply defined and was occasionally obscured by high chlorophyll concentrations in the overlying water. These fluctuations are of considerable interest. Namias (1971) has investigated the meteorological and oceanographic conditions accompanying a vast pool of abnormally warm water in the southern portions of the North Pacific during the summer and fall of 1968. He concludes:

> The abrupt and extensive anomalous warming of the southeastern quarter of the Pacific Ocean north of 20°N from May-June, 1968, appears to have been due largely to increased isolation and horizontal convergence of the surface layers of the sea and associated downwelling, ... These warming factors in the heat budget were associated with the development and maintenance of a strong and deep Pacific anticyclone in June which appears to have been persistently regenerated by an unusually strong mean jet around 40°N.

This period of stronger subsidence was accompanied by a clear sharpening of the maximum layer and by reduced standing crop of phytoplankton and productivity above the layer. The observations of Namias suggest that the generalized downwelling in the Central North Pacific anticyclone, which is an important factor inhibiting the vertical diffusion of nutrients into the euphotic zone, is also closely related to the depth and concentration of photosynthetic material below the mixed layer. Extrapolation leads us to expect to find similar chlorophyll maxima well developed in other large, persistent temperate gyres, such as the South Atlantic and the southern Indian Ocean.

DISCUSSION

It is evident that a deep chlorophyll maximum layer is a well-developed and consistent feature of the major gyres of both the North and South Pacific. In view of its geographic continuity, we must reevaluate the mechanisms postulated for its development, and seek a single explana-

tion to account for the presence of a chlorophyll maximum layer in very different environmental regimes. Of the numerous hypotheses which have been put forward, several may be relevant. The increase of chlorophyll with depth corresponds to an increase in the number of phytoplankton (diatom) cells, but this may be accentuated by an increase in the amount of chlorophyll per cell. Zooplankton have been shown to be concentrated above the maximum layer and differential grazing pressure may help to maintain the abrupt gradient at the top of the maximum layer. In situ production has been demonstrated within the maximum layer at very low light intensities, and this will contribute to the formation and maintenance of the layer.

The strong development of a deep maximum within the oligotrophic environments of the Central Gyres, the effect of fluctuations of the rate of downwelling on the depth of the maximum layer and the productivity in the overlying water, and the consistent relationship between the depth of the maximum layer and the depth of the nutricline and the nitrite maximum suggest that the nutrient regime may be a critical factor in the development and maintenance of the chlorophyll maximum layer. Our observations to date support the theory of Steele and Yentsch (1960) that depletion of nutrients above the summer thermocline leads to a reduction in the buoyancy of phytoplankton, and that a subsurface maximum results from the accumulation of impoverished cells at the top of the nutricline where the absorption of nutrients decreases the sinking velocity (Eppley, Holmes, and Strickland, 1967). The maximum layer may continue to subside slowly as the nutrients at the top of the nutricline are depleted, and thus it may be that the depth of the maximum layer is ultimately determined by the nutrient regime, rather than ambient light intensity. As long as the depth does not exceed the maximum depth of the winter mixed layer the cells will be returned to higher light levels during the winter. It may be that the chlorophyll maximum layer represents a senescent stage in the annual cycle of oceanic phytoplankton which is analogous to the formation of resting spores by many neritic species.

It is evident that the chlorophyll maximum layer, which may account for a major portion of the standing crop of plant material and for a substantial portion of the primary productivity, is not restricted to the traditionally defined "euphotic" zone, the zone above the 1% light level. There is no justification for limiting samples for chlorophyll or productivity measurements to this zone. These programs must be extended below the chlorophyll maximum layer. We expect this will result in a substantial increase in the estimates of total production within the water column.

ACKNOWLEDGMENTS

The work was supported in part by National Science Foundation Grant GB-12413 and in part by the Marine Life Research Program, the Scripps Institution of Oceanography's part of the California Cooperative Oceanic Fisheries Investigations, which are sponsored by the Marine Research Committee of the State of California, and by the National Science Foundation Grant GB-2861.

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THE NAUPLIUS II, METANAUPLIUS, AND CALYPTOPIS STAGES OF *THYSANOPODA TRICUSPIDATA* MILNE-EDWARDS (EUPHAUSIACEA)

MARGARET D. KNIGHT[1]

ABSTRACT

A large, spinose metanauplius, a nauplius II, and calyptopis I, found in the Indian Ocean and Equatorial Pacific, are referred to *Thysanopoda tricuspidata*. The identifications are based on the distinctive morphological features shared by these larval stages and by the calyptopes II and III of *T. tricuspidata* identified by Sars (1885), and on the observed distribution of *T. tricuspidata* and the metanauplius in the Indian Ocean. Calyptopes II and III are redescribed to present the complete calyptopis phase of larval development in one account.

During a survey of euphausiids in the Indian Ocean (Brinton and Gopalakrishnan, in press), many specimens of a relatively large and very ornate metanauplius were found. There was conjecture that the curious, apparently undescribed form might be the larva of a species of the genus *Thysanopoda*, and it was sought for next in plankton from the Equatorial Pacific.

The metanauplius was found in these waters as were specimens of a seemingly related nauplius II and calyptopis I together with the calyptopis II, calyptopis III, furcilia, and juvenile stages of *Thysanopoda tricuspidata* identified by Sars (1885). When individuals of each of the larval stages were placed together, they appeared to form a natural developmental series; their relative size, the distinctive shape of developing eyes, telson, and carapace all suggested that the larvae were progressive stages of the same species. Evidence of their specific relationship was found in a detailed study of these features and of the morphology of larval appendages, and there seemed to be sufficient justification for referral of the three unidentified early stages to *T. tricuspidata*.

Redescriptions of the calyptopes II and III of *T. tricuspidata* are included in this paper with identification and description of the nauplius II, metanauplius, and calyptopis I, in order to present the complete calyptopis phase of the species in one account and to illustrate the setation of appendages more fully.

METHODS AND MATERIALS

Specimens of the metanauplius were observed in the standard collections, approximately 200-0 m depth, obtained during the International Indian Ocean Expedition (IIOE), 1962-65. About 100 metanauplii were removed for study. The distributions of *T. tricuspidata* and the metanauplius based on the data of Brinton and Gopalakrishnan are shown in Figure 9.

Selected samples taken during EQUAPAC Expedition by RV *Stranger* of the Scripps Institution of Oceanography in August-September 1956 between long 165°-175°W and lat 6°S-10°N by oblique tow in the top 200 m (Snyder and Fleminger, 1965) were sorted for the metanauplius and calyptopes. Positions of the samples yielding larvae and the developmental stages found in each sample are given in Table 1. The distribution of *T. tricuspidata* in the Pacific is described by Brinton (1962).

For measurement with an ocular micrometer, the larvae were straightened in a few drops of

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TABLE 1.—Location of samples collected by RV *Stranger* during EQUAPAC Expedition which contained larvae of *Thysanopoda tricuspidata* and the developmental stages found. Detailed station data for samples are given by Snyder and Fleminger (1965).

Station No.	Position		Sample (net)	Developmental stage				
	Lat	Long		Nauplius	Metanauplius	Calyptopis		
						I	II	III
15	5°59′N	166°40′W	45 cm	−	+	+	+	−
21	0°00′N	166°55′W	45 cm	−	+	−	−	−
25	4°00′S	167°03′W	45 cm	−	+	+	+	+
25	4°00′S	167°03′W	1 m	−	+	+	+	+
26	5°00′S	167°08′W	45 cm	+	+	+	+	+
26	5°00′S	167°08′W	1 m	+	+	−	+	+
28	5°58′S	175°02′W	45 cm	+	+	+	+	+
28	5°58′S	175°02′W	1 m	+	+	+	−	+
28	5°58′S	175°02′W	1 m	+	+	+	+	−
29	5°01′S	174°59′W	45 cm	−	+	−	+	+

2% formaldehyde in seawater on a slide. Total length (TL) was measured in dorsal view between center of anterior margin of carapace (excluding spines in metanauplius) or rostrum and distal point on posterior margin of telson excluding spines. Other measurements are explained by stage: nauplius II, width (W) at widest point in dorsal view; metanauplius, carapace length (CL) between midpoints of anterior and posterior margins excluding spines, carapace width (CW) at widest point between anterolateral margins excluding spines, both measured in dorsal view; calyptopes I and II, carapace length (CL) between midpoints of anterior and posterior margins measured in lateral view; calyptopis III, carapace length (CL) from rostrum to distal point on posterior margin measured in lateral view. The range (r) and mean (m) of each measurement and number (n) of specimens measured are given by stage.

Approximately equal numbers of the metanauplius stage from the Indian and Pacific Oceans were measured. The measurements given for nauplius II and calyptopes I-III, however, are based only on larvae from the Equatorial Pacific and, as calyptopis larvae of a single species have been shown to vary in size in different areas of the oceans (Mauchline and Fisher, 1969), it should be emphasized that the larvae measured for this study were collected during one season in one area of the Pacific. Measurements of some nauplius II and calyptopis stages sorted from Indian Ocean samples did fall well within the size ranges of Pacific larvae in equivalent developmental stages. Specimens of a nauplius I definitely referable to *T. tricuspidata* were not found.

For detailed study and dissection of appendages, larvae were placed in glycerine. Some were stained with Chlorazol Black E to clarify appendage setation. Fourteen nauplii and at least 20 individuals of each of the metanauplius and calyptopis stages I-III were examined in detail. At least 10 specimens of each stage were dissected for study of appendages. In a study of the larval development of *Nematoscelis difficilis* based on both larvae reared in the laboratory and larvae from the plankton, Gopalakrishnan (in press) found no variability in form or setation of appendages among individuals at the same stage of development. This also appears to be true of *T. tricuspidata* larvae, in the stages described, with respect to the mouthparts where setation is usually intact in preserved specimens. On antennules, however, the terminal setae, spines, and aesthetascs (sensory setae) were frequently broken; in calyptopis II, for instance, only 1 of 26 antennules examined had the third seta intact on the inner and outer flagella. An estimate of variability in the fragile setation in this species will require a detailed study of larvae either reared in the laboratory or collected specifically for the purpose.

Drawings of both whole larvae and appendages were prepared with the Wild M20[2] com-

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

pound microscope equipped with drawing attachment.

Nomenclature for description of appendages is based on that of Gurney (1942). For a review of the literature on larval development of the Euphausiacea and the nomenclature of their larval phases, the reader is referred to the papers by Gopalakrishnan (in press) and by Mauchline and Fisher (1969).

RESULTS

DESCRIPTION OF DEVELOPMENTAL STAGES

Nauplius II (Figure 1a, b)

Measurements: TL, r = 1.00-1.12 mm, m = 1.06 mm; W, r = 0.48-0.56 mm, m = 0.53 mm; n = 43.

Body oval, about 2 times as long as wide, anterior pointed, posterior truncate; posterior margin armed with 10 spines—3 pairs of posterolateral spines and 2 pairs of small to rudimentary medial terminal spines, posterolateral spine 1 (outer) is small, spines 2 and 3 are relatively large, only spine 3 (inner) bears spinules.

Antennule (Figure 4a) uniramous; with 2 terminal setae, 1 subterminal seta situated medioventrally, and small spiny prominences at base of each seta—that below largest terminal seta is like small lobe; spinules are distributed on surface as figured.

Antenna (Figure 5a) biramous; protopod may be constricted near middle and appear weakly segmented; endopod unsegmented with 3 terminal plumose setae, a rudiment of 4th terminal seta, 1 subterminal seta on inner margin, and rows of spinules at bases of setae; exopod with outer margin divided into about 10-11 segments (the segmentation was often indistinct in most distal and proximal parts of exopod), the 5 distal segments bear plumose setae—the terminal segment has 2 setae with a few spinules and the remaining 4 segments bear 1 seta each.

Mandible (Figure 6a) biramous and unsegmented; both rami bear 3 plumose setae with spinules at base of setae.

In well-developed nauplii nearing molt to metanauplius, the carapace of the metanauplius with its distinctive ornamentation could be seen inside the cuticle of the nauplius (Figure 1a), both the large long spines around the anterior margin which fold up and back around the body and the 4 large medial and smaller posterolateral spines on posterior margin may be visible and may be partially dissected out.

Metanauplius (Figure 1c, d)

Measurements: Equatorial Pacific larvae - TL, r = 1.36-1.50 mm, m = 1.43 mm; CL, r = 1.02-1.10 mm, m = 1.05 mm; CW, r = 0.60-0.70 mm, m = 0.64 mm; n = 39. Indian Ocean larvae - TL, r = 1.36-1.52 mm, m = 1.45; CL, r = 0.98-1.10 mm, m = 1.05 mm; CW, r = 0.61-0.68 mm, m = 0.65, n = 43.

Carapace with rounded frontal and anterolateral margins produced into long spines (the number of spines, counted in 25 individuals, ranged from 21 to 23 with 23 larvae having 22 spines), there may be tiny spines or "hairs" posterior to the posteriorly directed last large spine; posterolaterally deep winglike extensions of carapace curve ventrolaterally with margins produced into strong posteriorly directed spines which diminish in size around posterior margin where they are separated by small spines; the 4 large medial spines on posterior margin are usually relatively long and they project up dorsally away from body of larva. A faint outline of developing eyes is visible. Tail long and tapering with rounded posterolateral margins and median indentation, there is now a pair of lateral spines in addition to 3 pairs of posterolateral spines and 2 pairs of medial terminal spines, a small rudiment of one or both of inner (third) pair of terminal spines may be present.

In one well-developed metanauplius near molt, the telson of calyptopis I with invaginated terminal and lateral spines was visible beneath the cuticle (Figure 1e). As can be seen, posterolateral spine 3, although shorter than spine 2 in the metanauplius, is more deeply invaginated and longer than spine 2 in the developing calyptopis, and when extruded, it will have the greater relative length observed in the calyptopis stages of *T. tricuspidata*.

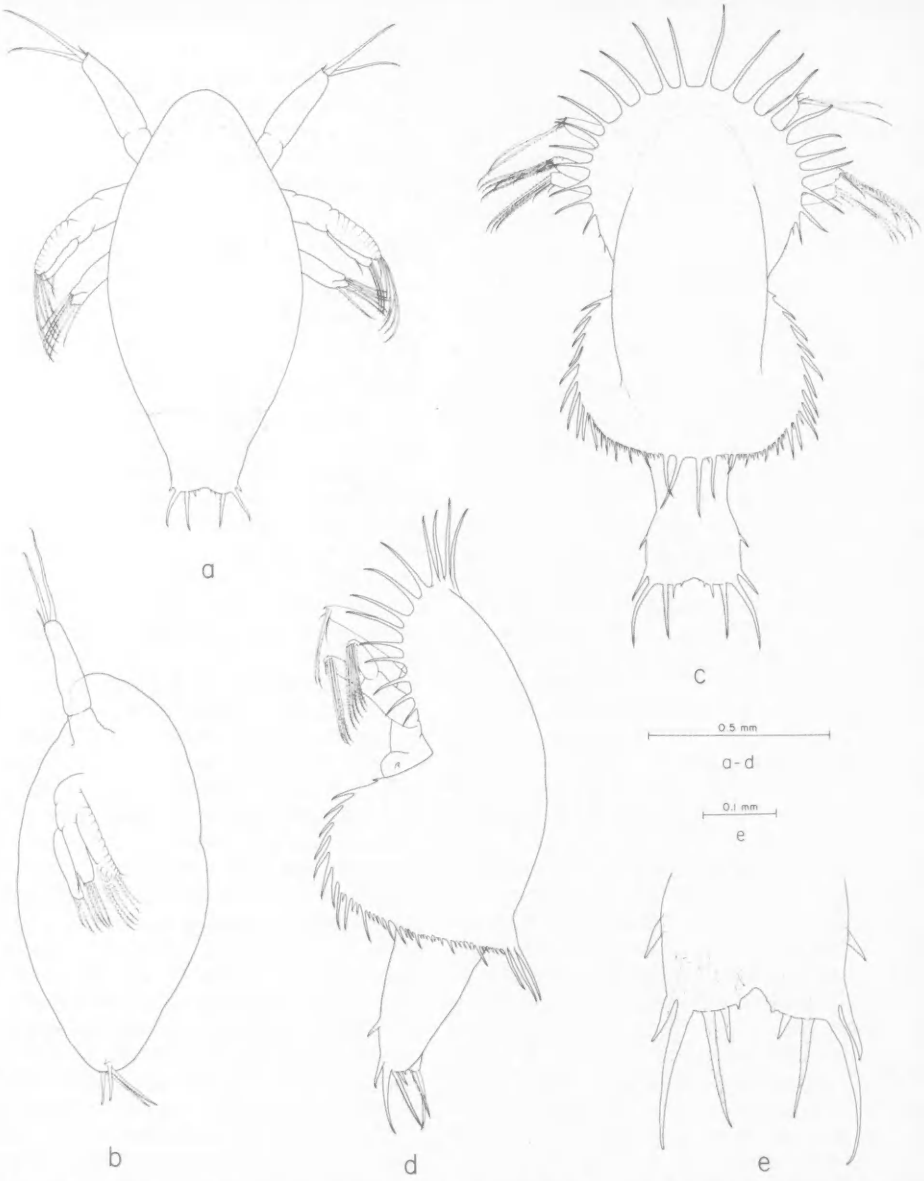
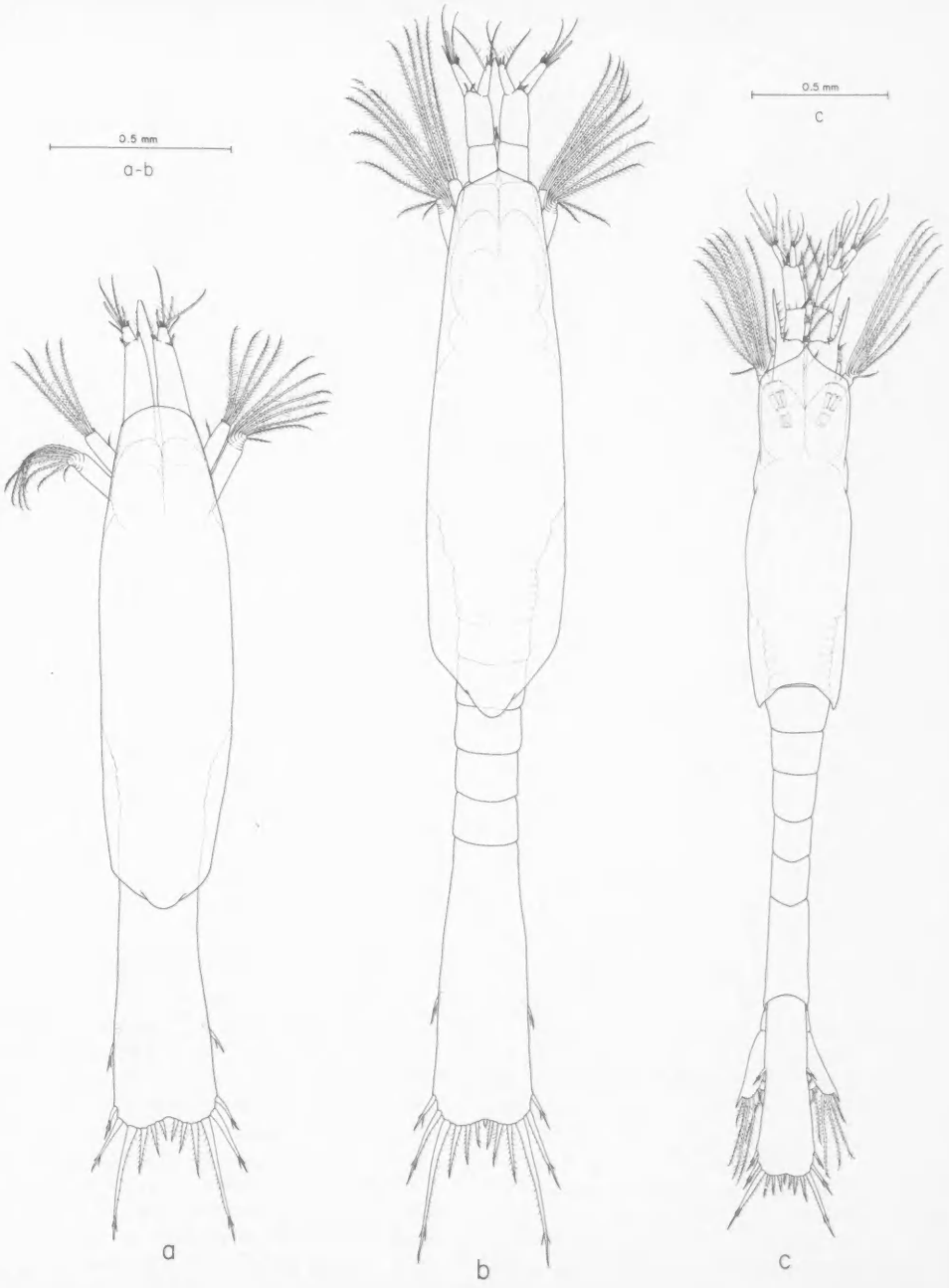


FIGURE 1.—Nauplius: a-b, dorsal and lateral views. Metanauplius: c-d, dorsal and lateral views; e, posterior enlarged showing invaginated spines of calyptopis I beneath cuticle.

FIGURE 2.—Calyptopis: a-c, stages I-III, dorsal views.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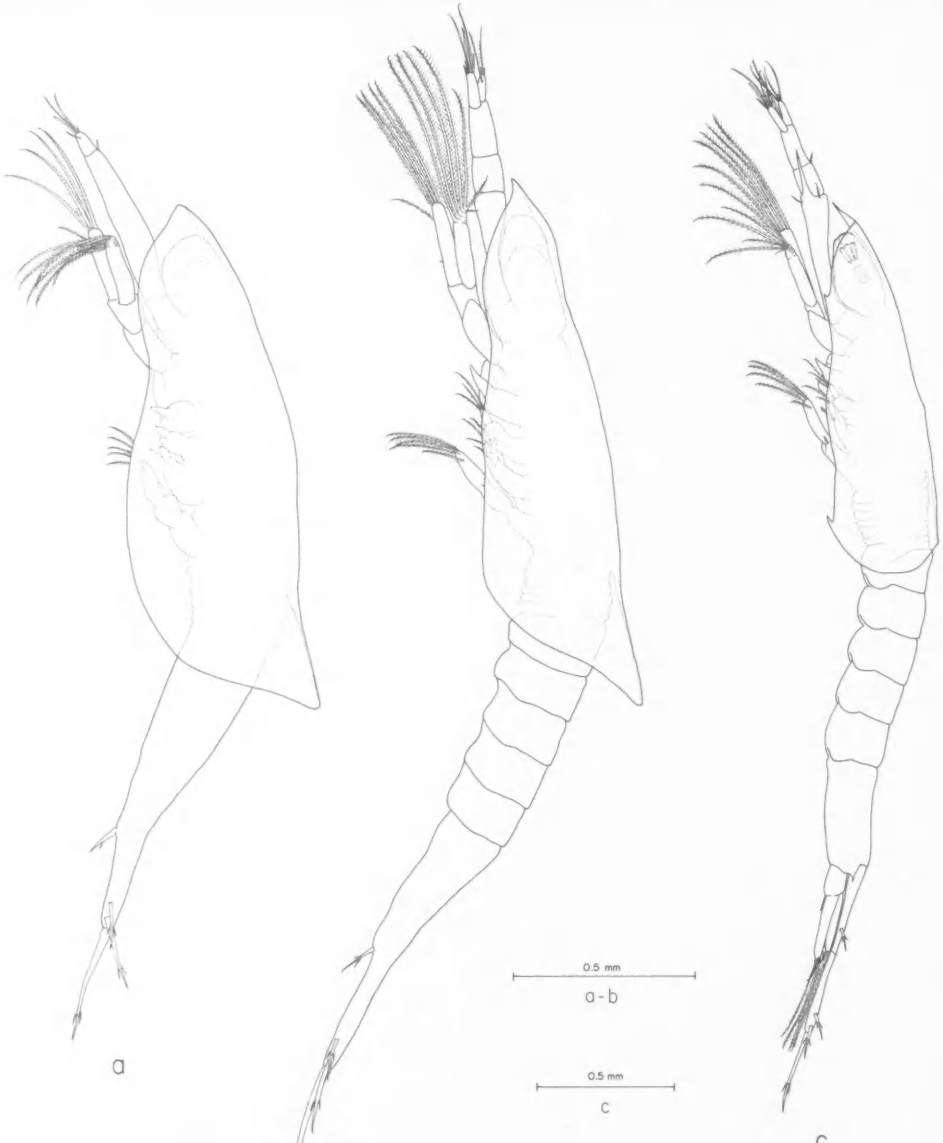

FIGURE 3.—Calyptopis: a-c, stages I-III, lateral views.

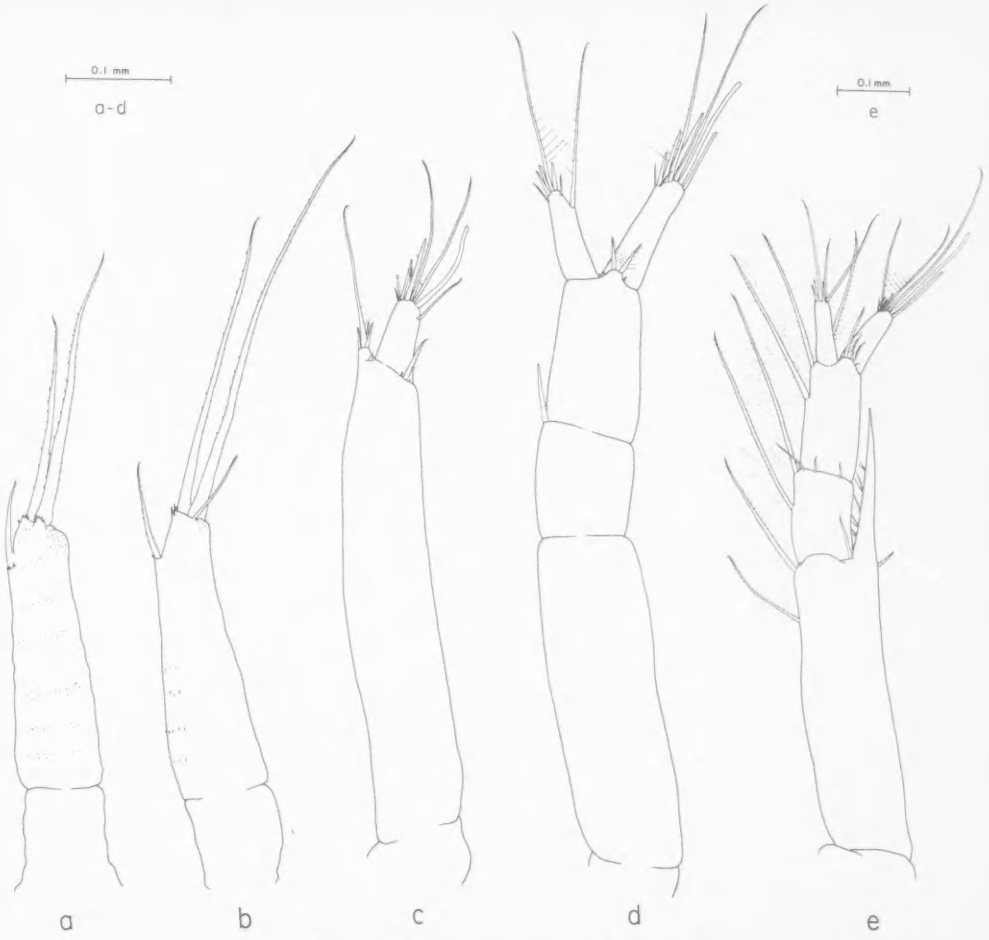

FIGURE 4.—Antennule, right, dorsal view: a, nauplius; b, metanauplius; c-e, calyptopes I-III.

Antennule (Figure 4b) now with 3 terminal processes, there is a small seta or sensory filament in place of spiny lobe; surface spinules appear to be organized into fewer simpler rows.

Antenna (Figure 5b) with protopod segmented into coxa and basis, there are a few spinules on inner distal margin of each; endopod with 4 terminal setae—1 seta is relatively short, and 2 setae on inner margin—the proximal seta is short to rudimentary; exopod with 5 short terminal segments but without proximal segmentation of outer margin seen in nauplius, the setation is unchanged although there may be a spinous rudiment of third seta on terminal segment.

Mandible (Figure 6b) reduced to rounded lobe bearing pointed lateral process.

Maxillule, maxilla, and maxilliped are represented only be rounded prominences. In specimens nearing molt, the rudimentary spines on endopod and endites of developing maxillules and

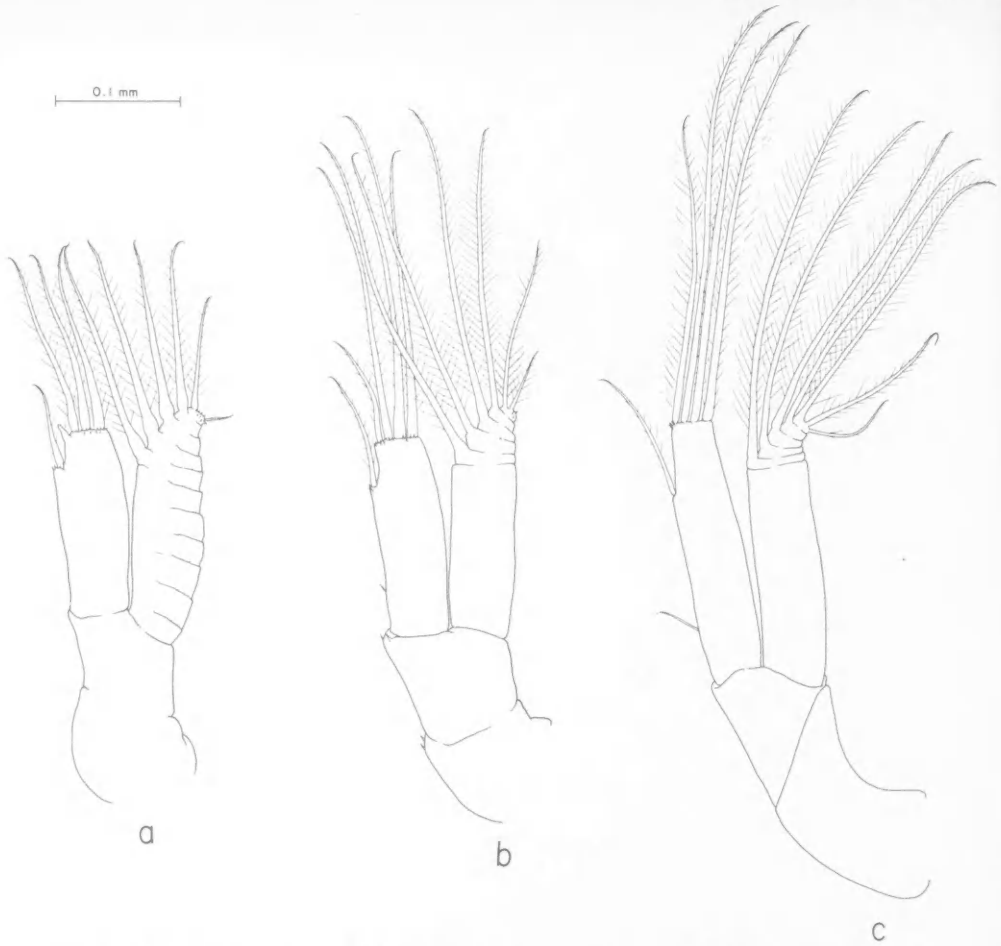

FIGURE 5.—Antenna, right, anterior view: a, nauplius; b, metanauplius; c, calyptopis I.

maxillae and setae of biramous maxilliped of calyptopis I may be seen through the cuticle. Figure 7a and d show such a maxillule and maxilla dissected from a metanauplius providing evidence of its relationship with the calyptopis I described.

Calyptopis I (Figures 2a, 3a)

Measurements: TL, r = 1.90-2.16 mm, m = 2.07 mm; CL, r = 1.38-1.48 mm, m = 1.44 mm; n = 34.

Carapace long and slender, without spines, anterior margin forming narrow hood over developing eyes, posterior margin pointed and curving dorsally. Abdomen unsegmented, telson with a pair of lateral spines, 3 pairs of posterolateral spines, and 3 pairs of medial terminal spines, posterolateral spine 3 is now longest; posterior margin curves in medially.

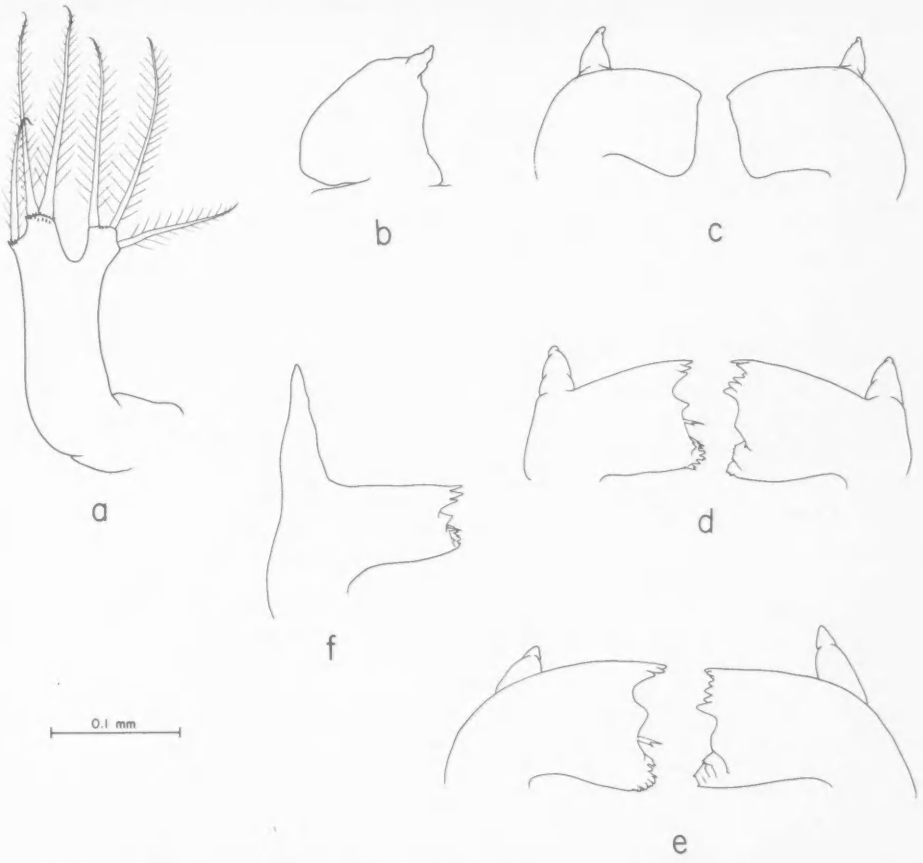

FIGURE 6.—Mandible: a, nauplius, right, anterior view; b, metanauplius, left, posterior view. Mandibles, posterior view: c-e, calyptopes I-III; f, right mandible of calyptopis II rotated to show relative length of triangular lateral process.

Antennule (Figure 4c) 2-segmented; protopod long and slender with small terminal segment forming outer flagellum which bears about 9 terminal processes including 2 long setae, 2 aesthetascs (one of these is situated slightly subterminally on outer margin), and about 5 spinous processes of varying sizes; there is rudiment of inner flagellum bearing 1 long seta and 3 spinous processes; a small spine is situated at base of inner ramus, and there is 1 seta and 1 or 2 small spines dorsally on distal margin of protopod at base of outer flagellum.

Antenna (Figure 5c) now with form found in calyptopis stages I-III; endopod with 4 long terminal setae and 2 setae on inner margin, proximal seta still relatively short; exopod with 7 plumose setae, the terminal segment now bears 3 setae; coxa and basis without spinules.

Mandibles (Figure 6c) rudimentary, with large lateral process, medial margins smooth except for 1 small incisor tooth on each mandible.

Maxillule (Figure 7b) armed only with rudimentary small spines; endopod of 1 segment with 3 spines; exopod a very small lobe bearing

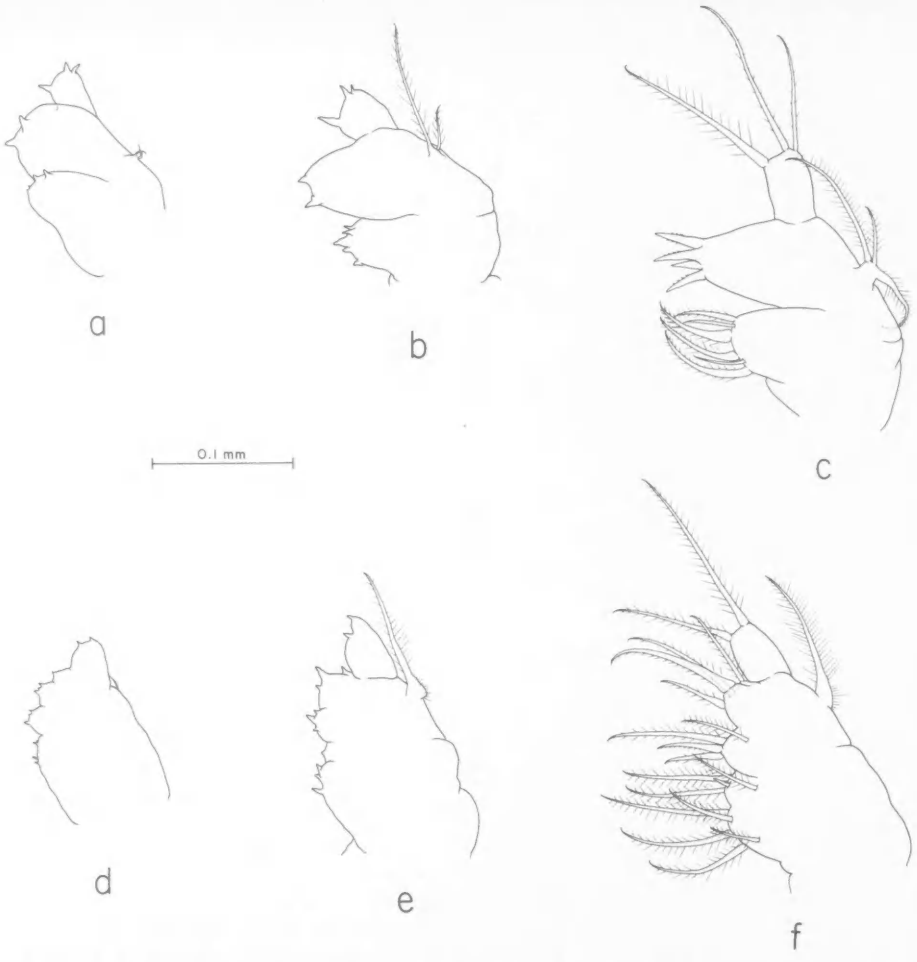

FIGURE 7.—Maxillule, left, posterior view: a, developing appendage of calyptopis I dissected from metanauplius; b-c, calyptopes I and II. Maxilla, left, posterior view: d, developing appendage of calyptopis I dissected from metanauplius; e-f, calyptopes I and II.

2 plumose setae; basal endite with 2 spines, there may be a tiny third spine between large spines; coxal endite with about 5 spines.

Maxilla (Figure 7e) with rudimentary setation except for 1 plumose seta arising from small finely setose lobe on lateral margin and representing exopod; endopod of 1 segment with 2 spines; medial lobes of endites discernible with small spines on medial margin.

Maxilliped (Figure 8a) biramous; exopod with 4 terminal plumose setae and 1 subterminal seta on outer margin, also a small stout seta at base of exopod near articulation with basis; endopod of 2 segments, terminal segment with 4 setae distally, 3 terminal and 1 subterminal; there are a few weak setae and rudiments of setae on medial margins of both coxa and basis and of proximal segment of endopod.

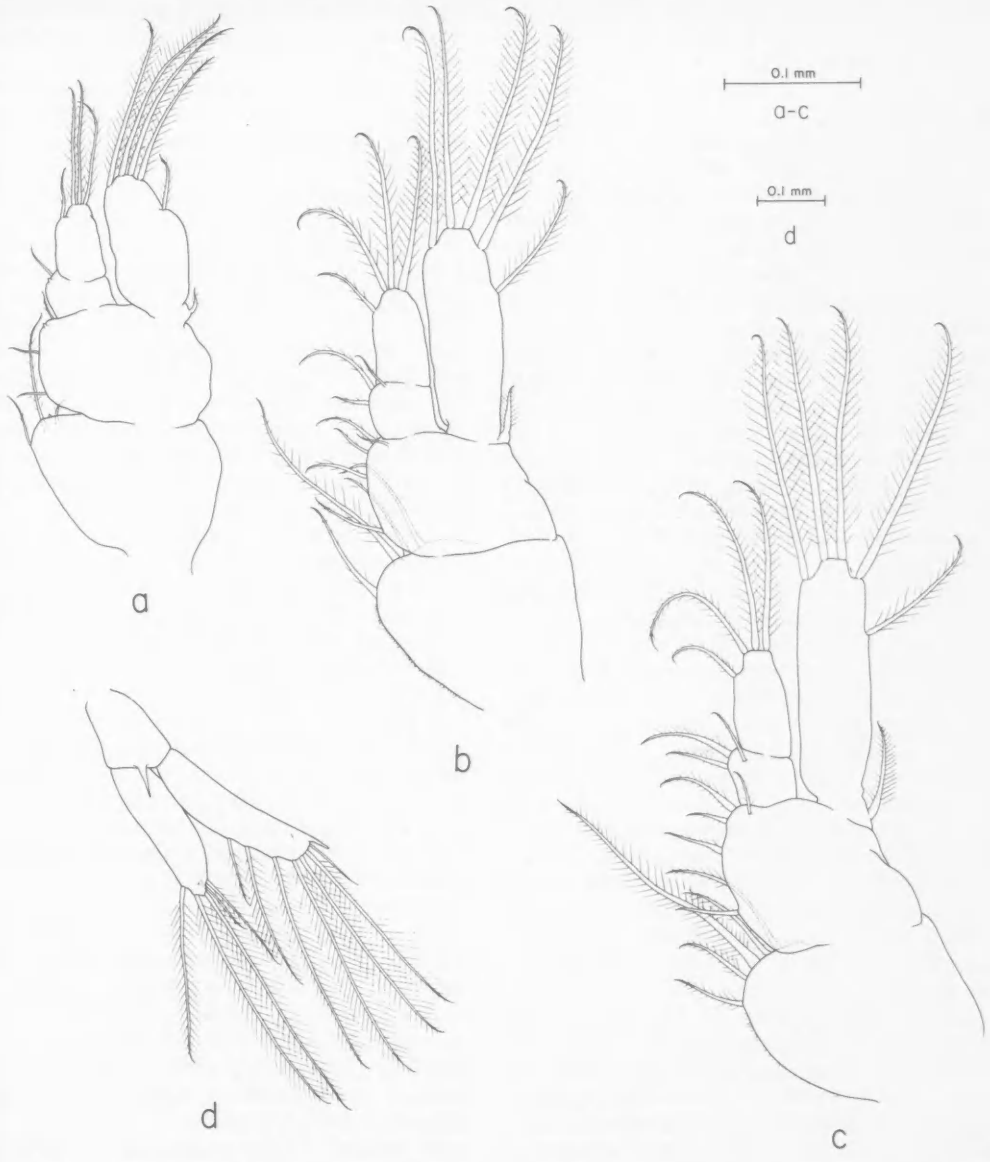

FIGURE 8.—Maxilliped, left, posterior view: a-c, calyptopes I-III. Uropod, left, ventral view: d, calyptopis III.

Calyptopis II (Figures 2b, 3b)

Measurements: TL, r = 2.50-2.74 mm, m = 2.63 mm; CL, r = 1.42-1.54 mm, m = 1.49 mm; n = 18.

Carapace with frontal margin produced into small triangular spine and posterior margin more pointed than in preceding stage; developing eyes may contain some pigment. Thoracic segments forming; abdomen segmented, sixth segment not separate from telson; posterior margin of telson with small median 7th terminal spine.

Antennule (Figure 4d) with protopod divided into 3 peduncular segments, there is stout seta distally on inner margin of second segment and a small dorsal lobe bearing 2 setae and a few small spines on distal margin of third segment at base of outer flagellum; outer flagellum with about 9 terminal processes including 2 setae, 2 aesthetascs, and about 4-6 spinous processes; inner ramus with about 6 terminal processes including 1 seta and usually 5 spines, there is 1 subterminal seta on inner margin.

Antenna as in calyptopis I.

Mandibles (Figure 6d) asymmetrical, now differentiated into incisor and molar areas, right mandible with slender articulated spine with spinule situated near molar area; right mandible rotated in Figure 6f to show relative length of lateral process.

Maxillule (Figure 7c) with setae and spines fully formed; endopod of 1 segment with 3 setae; exopod with 3 plumose setae; basal endite with 4 stout spines armed with spinules; coxal endite with 6 setae—2 are small smooth setae, 4 are setose and the largest bears strong spinules distally.

Maxilla (Figure 7f) with full setation; endopod of 1 segment with 2 setae; exopod represented by a single plumose seta on small setose lobe; basal endite with 3 medial lobes, coxal endite bilobed, lobes 1-5 with setation of 5-4-4-3-1 progressing distally, 1 seta on each of lobes 1-3 is situated on posterior face of maxilla, 1 marginal seta on lobe 2 is quite small.

Maxilliped (Figure 8b) now with full medial setation; coxa with 4 plumose setae, 1 seta is relatively long; basis with 5 setae; proximal segment of endopod with 3 setae; 1 distal seta on basis and 1 distal seta on first segment of endopod are situated slightly submarginally on posterior face, both are small and frequently difficult to locate; setation of exopod and terminal segment of endopod is unchanged.

Calyptopis III (Figures 2c, 3c)

Measurements: TL, r = 2.90-3.40 mm, m = 3.14 mm; CL, r = 1.30-1.42 mm, m = 1.35 mm; n = 34.

Larva now appears more slender for its length; carapace considerably altered, still forming narrow hood over eyes but in other respects more like carapace of furcilia, frontal margin produced into small triangular rostrum, lateral margins with small anterolateral spine below eye and large posterolateral denticle, posterior dorsal margin no longer tapering to point but indented medially. Eye with 7 well-developed facets arranged in a circle of 6 with seventh central facet, and ommatidia with pigment. Thoracic segmentation more distinct. Abdomen with 6 segments, there is dorsal ridge or fold around segment 1 and segment 6 carries biramous uropods. Setation of telson unchanged.

Antennule (Figure 4e) with distal lateral margin of basal peduncular segment produced into strong lateral spine which extends to or beyond midpoint of distal segment of peduncle; there are about 5 groups of 2 setae each along inner margin of this spine with spinules between 3 distal groups and a seta at base of spine on both outer and inner margins; basal segment of peduncle dorsoventrally flattened; the peduncular segments bear plumose setae along medial margins with 2-2-3 setae on segments 1-3 respectively, there are 3 small setae around distal margin of segment 2, and 3 setae and setules on dorsal lobe below outer ramus on distal margin of segment 3; outer flagellum with 2 aesthetascs, 3 setae, and about 4 small spines; inner flagellum with 3 terminal setae and about 3 spinous processes.

Antenna as in calyptopis I.

Mandibles (Figure 6e) similar to calyptopis II, medial teeth somewhat flattened.

Maxillule and maxilla as in calyptopis II.

Maxilliped (Figure 8c) with 5 setae on medial margin of coxa; there is no other change in setation.

No rudiment of the second thoracic appendage was observed.

Uropod (Figure 8d) biramous; protopod with stout ventral spine; exopod produced into posterolateral spine and bearing 7 plumose setae around posterior and medial margins, the seta near posterolateral spine is relatively small; endopod with 5 distal plumose setae, 1 seta is situated submarginally and projects dorsally.

IDENTIFICATION OF EARLY STAGES

The morphological evidence on which the identification of the larval series is based may be summarized as follows: 1) the nauplius II is linked to the metanauplius by dissection of the spinose carapace of the metanauplius from well-developed nauplii; 2) the metanauplius and calyptopes I-III are related by the setation of mouthparts, particularly the endopods of maxillule and maxilla; 3) the third calyptopis is identified with the larva described by Sars (1885) by the long and slender body, the distinctive 7-facetted eyes, and the setation of the exopod and 1-segmented endopod of the maxillule which bear 3 setae each.

There is additional evidence to support the identification of the metanauplius in the way in which the observed distribution of the larva corresponds with that of *T. tricuspidata* in the Indian Ocean as shown in Figure 9, and in the occurrence of the larvae within the range of *T. tricuspidata* in the Pacific.

DISCUSSION

The only description of *T. tricuspidata* larvae found which deals with the calyptopis stages is that of Sars (1885); other authors referring to larvae of the species (i.e., Tattersall, 1936; Gurney, 1947; Lebour, 1950; Pillai, 1957) discuss the furcilia stages only. Sars provides some details of setation with his general descriptions and figures the mandible, maxillule, maxilla, and maxilliped of the third calyptopis (1885, Plate 21, Figures 13-16). The mouthparts of the calyptopis III described in this study agree with those figured by Sars in the dentition of left mandible, in segmentation and setation of endopod and exopod of maxillule, in rudimentary exopod of maxilla, and in setation of exopod and terminal segment of endopod of maxilliped. The carapace of Sars' calyptopis III appears to be indented medially on the posterior margin rather than pointed as in calyptopis II, but it is not figured with a lateral denticle.

The descriptions of larvae of other species of the genus *Thysanopoda* are also almost entirely limited to the furcilia phase; only two exceptions were found. Einarsson (1945) described the calyptopes II and III of *T. acutifrons* and Lebour (1950) the calyptopis III of *T. cristata*, but figures of the appendages and the details of setation are not given.

The described larvae of *T. acutifrons* are larger than those of *T. tricuspidata* in equivalent stages; calyptopes II and III measure 3.4 and 3.8 mm in total length respectively while *T. tricuspidata* averages 2.6 and 3.1 mm (Sars' specimens measured 2.5 and 3.5 mm). The carapace of the third calyptopis of *T. acutifrons* is like that of the second calyptopis with "characteristic pointed end," and the lateral denticle is sometimes discernible although very small. Einarsson notes that the maxillule has a palp of 2 segments and an inner lobe with 7 bristles. Frost (1939) figures the appendages of the first furcilia of *T. acutifrons* showing the maxillule with 6 setae on the endopod and 4 setae on the exopod, and the endopod of the maxilla with 3 setae. This setation is probably also found on the calyptopis III of the species she describes. [Einarsson (1945) suggested that, based on the shape of the eye, Frost's larvae may instead belong to *T. microphthalma*; he notes, however, that the species are otherwise alike in development.]

Lebour (1950) describes and figures the carapace of the calyptopis III of *T. cristata* as long and "pointed behind," noting that the larva closely resembles the calyptopis III of *T. acutifrons* described by Einarsson. It is also very large, measuring 4.2 mm in length. Gurney (1947), in his description of the first furcilia

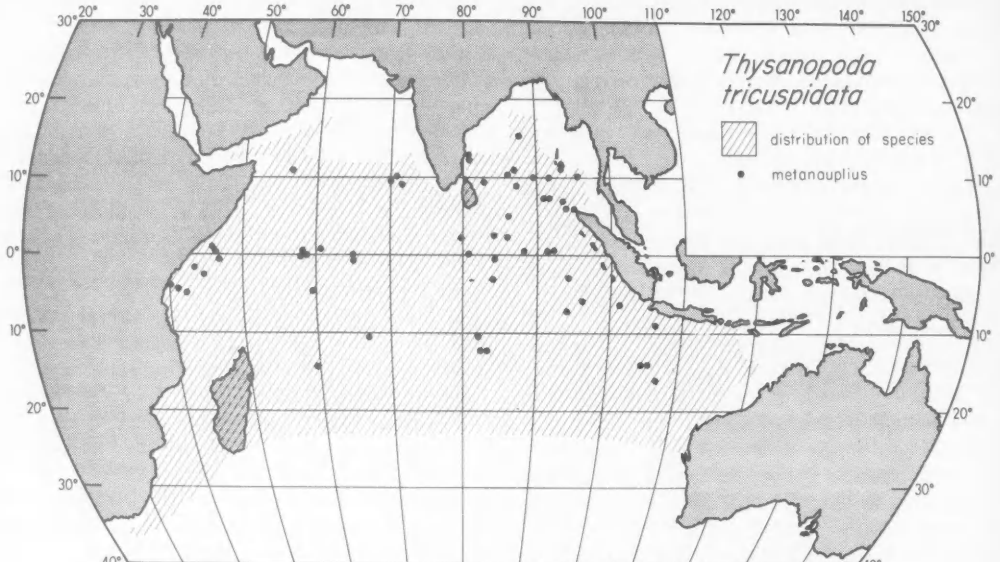

FIGURE 9.—The distribution of *Thysanopoda tricuspidata* and the metanauplius larva in the Indian Ocean based on the analyses of Brinton and Gopalakrishnan (in press).

of *T. cristata*, notes that the maxillule has an endopod of 2 segments, and again it seems likely that this is also found in the third calyptopis.

Both *T. acutifrons* and *T. cristata*, then, differ from *T. tricuspidata* in length of described stages, in shape of carapace in calyptopis III, and probably in details of segmentation and setation of maxillule and maxilla at least.

Calyptopes I and II of *T. monacantha* (identified by E. Brinton) were dissected to compare the endopods of the maxillule and maxilla with those of calyptopes I and II of *T. tricuspidata*. The calyptopis I had full setation of mouthparts and, in both stages, the maxillule, like that of Frost's furcilia, had an endopod of 2 segments with 6 setae and exopod with 4 setae, and there were 3 setae on the endopod of the maxilla. In fact, more setae were found on all of the mouthparts of the *T. monacantha* larvae with the exception of the endopod and exopod of the maxilliped which were like those of the *T. tricuspidata* calyptopes.

Information in these few accounts from the literature and from personal observation suggest that *T. tricuspidata* larvae may prove to differ from larvae of other species of the genus

in many respects. The partial segmentation of antennal exopod in the nauplius II and the form and armature of carapace and telson of the metanauplius may be distinctive, the rudimentary setation of mouthparts in calyptopis I appears to be unusual—indeed the larva seems ill-equipped to feed, there seems to be a reduction in dentition of mandibles and in numbers of setae on mouthparts in calyptopes II and III, and the carapace of calyptopis III is transitional between the usual calyptopis and furcilia forms. In addition, the larvae are known to deviate from trends within the genus in development of abdominal pleopods during the furcilia phase. According to Lebour (1950), *T. tricuspidata* is the most variable in pleopod succession of any *Thysanopoda* species, indeed of any euphausiid known and, as it has been demonstrated that there is a correlation between a more rigidly defined number of furciliar stages and a more oceanic distribution within the genus *Thysanopoda* (Mauchline and Fisher, 1969), such variability in the oceanic species *T. tricuspidata* is surprising.

Although there is too little information available at this time for speculation as to the significance of the unusual morphological features observed in this study, the details found in the literature did support the identification of the larvae in that the combination of setation of endopod and exopod of the maxillule and endopod of the maxilla of *T. tricuspidata* calyptopes was not noted or figured in descriptions of the larvae either of other species of *Thysanopoda* or of other genera of the family.

ACKNOWLEDGMENTS

I wish to thank E. Brinton for his assistance and criticism of the manuscript, and we both wish it to be known that the plankton sorting staff at the Indian Ocean Biological Centre first identified the unique metanauplius as a euphausiid.

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THE LARVAL STAGES OF THE DEEP SEA RED CRAB, *GERYON QUINQUEDENS* SMITH, REARED UNDER LABORATORY CONDITIONS (DECAPODA: BRACHYRHYNCHA)

HERBERT C. PERKINS[1]

ABSTRACT

A prezoeal stage, four zoeal stages, and one megalopa stage were obtained from eggs of *Geryon quinquedens* Smith hatched in the laboratory. Each zoeal stage and the megalopa are discussed and illustrated.

The commercial potential and abundance of the deep sea red crab, *Geryon quinquedens* Smith, are discussed by Schroeder (1959), McRae (1961), and Holmsen (1968). The red crab is obviously an important constituent of the deep-water benthic fauna found on the continental shelf off New England and the middle Atlantic states, and its larvae should therefore occur in considerable numbers in the plankton of that region. Knowledge of the larval stages of this species is apparently totally lacking. Brattegard and Sankarankutty (1967) have described the prezoea and the first zoea of *Geryon tridens* Kröyer from Norway, but I can find no other reference to the larval stages of this genus.

It is the purpose of this paper to describe the larval stages of *Geryon quinquedens* so that they may be identified in plankton collections and thus facilitate the understanding of the early life history of this species and hopefully to shed light on its apparently tenuous taxonomic status within the Brachyrhyncha.

METHODS AND MATERIALS

In February 1971, several berried females of *Geryon quinquedens* were captured in 300 fm of water (bottom temperature was 5.9°C) in the Baltimore Canyon area of the continental shelf (lat 37°56'N, long 73°55'W) off Delaware Bay. Three of the berried crabs were returned to the Boothbay Harbor Laboratory and maintained in shallow tanks at temperatures that ranged from 5° to 12°C. On 29 April 1971, one of the females died and some of her eggs were removed and placed in beakers of filtered seawater. Temperature in the beakers was 15°C; prezoeae were observed the next day and on 1 May first zoeae were apparent. On 10 May, another female's eggs started hatching in one of the tanks. Water temperature in this tank was 10°C. A prezoea stage was noted in the tank also but lasted less than 1 hr. First zoeae from each of these batches were maintained separately in beakers containing 1,000 ml of filtered seawater and 50,000 units of penicillin plus a small amount of streptomycin (some larvae were raised without the antibiotics with no differences noted). Newly hatched *Artemia* nauplii obtained from California eggs were given as food. Small amounts of algae (*Dunaliella*) were also added to sustain the *Artemia* nauplii. Water and food were changed every other day. At the start the zoeae were maintained at a constant temperature of 15°C, but fouling organisms grew on many of the zoeae and it was necessary to maintain them at room temperature (18°-21°C) to accelerate development. Salinity ranged 30 to 31‰ during the study. Zoeae were also put into compartmented plastic trays, one to a compartment, and were maintained as those in the beakers. The zoeae in the compartments were used for the developmental studies. When a zoea molted in a

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compartment it was preserved, along with its molt, the following day.

Measurements of the larvae were made with an ocular micrometer and are given in millimeters; drawings were made with the aid of a camera lucida. Ten individuals, of each stage, and their molts were examined and measured for the developmental series. Carapace length measurements were made from the anterior edge of the carapace (posterior edge of eye sockets) to the posterior margin, along the midline. Total length represents the distance from the tip of the rostral spine to the tip of the telson along the curves of the dorsal midline. The setae on some appendages have been shortened or deleted in some of the illustrations to ensure clarity, but are given full descriptions in the text.

RESULTS

A prezoea stage of short duration, four zoeal stages, and a megalopa stage were obtained. The prezoeae measured about 2.8 mm in total length. The following are the average number of days from one stage to the next at temperatures of 18° to 21°C; first stage zoea to second, 7 days; second to third, 6; third to fourth, 5; fourth to megalopa, 7; and megalopa to first crab, 14. Two abnormalities were observed; a first stage zoea with the protopodite of one antenna forked from the base, and a second stage zoea with the large lateral spine on one side of the telson forked from its base. The larvae are usually light reddish brown in gross appearance. Some individuals are quite light in appearance but both phases exhibit numerous melanophores scattered over the entire body, particularly on the cephalothorax and along the outer margins of the abdomen. Small melanophores are often scattered on the basipodite on the maxillipeds.

DESCRIPTION OF THE LARVAE

ZOEA I (Figure 1A)

Carapace length 0.83 mm (0.81-0.86); total length 3.71 mm (3.67-3.73). Carapace with rostral, lateral, and dorsal spines. Rostral spine strongly depressed; slightly longer than antennae and nearly three quarters the length of the dorsal spine. Lateral spines flexed slightly ventrad, broad based, and nearly as long as the rostral spine. Width of the carapace from tip to tip of lateral spines about half the total length of the body. Dorsal spine long and curved slightly posteriad; its length about one-third the total length of the body. A short slender seta is present on each side of the carapace, in line with the posterior margin of the dorsal spine's base. The eyes are not stalked. Abdomen with five somites and the telson (Figure 2H). Abdominal somites two through five with lateral spines (fifth somite in some individuals without spines); those on second somite fairly blunt and directed somewhat anteriad; spines on somites three through five sharper and hooked posteriad, decreasing in size posterially. Posterior lateral margin of somites three through five produced into long, sharp spines. Second somite with two setae on middorsal surface; somites three through five with two setae each on posterodorsal margin. Telson bifurcate with three pairs of setae on the inner side. Each furca with two lateral spines, one long and strong, the other much smaller, and a small dorsal spine. Antennule (Figure 2B) with four unequal aesthetes and a small seta terminally. The antenna (Figure 2A) bears a long protopodite with a row of spinules on the outer margins; the exopodite is about half the length of the protopodite and terminates in a spine and one seta. Mandible (Figure 2C) with two large teeth anteriorly, a medial blade, and a toothed edge posteriorly. The maxillule (Figure 2D) bears a two-segmented endopodite, the short proximal segment bears one long plumose seta, the distal segment with six long plumose setae, two of which are subterminal; the basal and coxal endites each bear six spinous setae. The scaphognathite of the maxilla (Figure 2E) has seven marginal plumose setae and a plumose apical tip; the endopodite is bilobed with five spinous setae on the distal lobe and three on the proximal; basal and coxal endites each bilobed with 5 + 5 and 3 + 3 spinous setae respectively. There is a suggestion of two segments in the exopodite of the first maxilliped (Figure 2F) which bears four, one-jointed, natatory setae terminally; endopodite

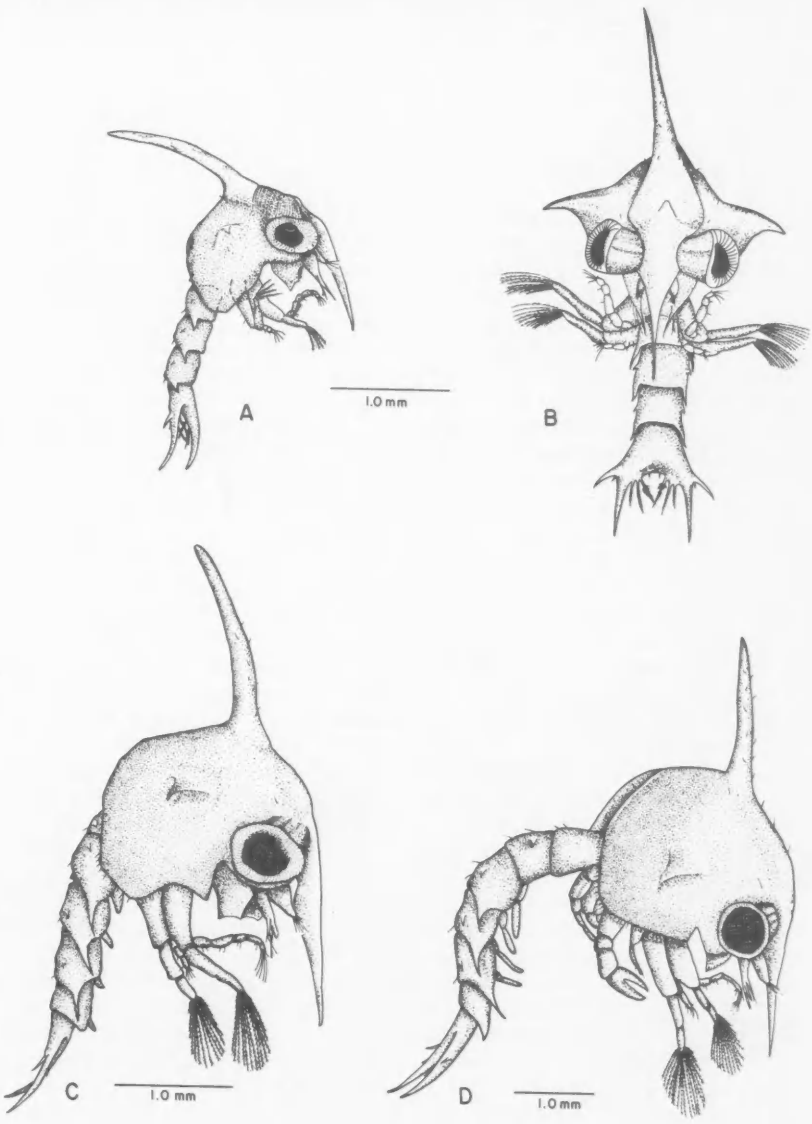

FIGURE 1.—*Geryon quinquedens*. A. Zoea I, B. Zoea II, C. Zoea III, D. Zoea IV.

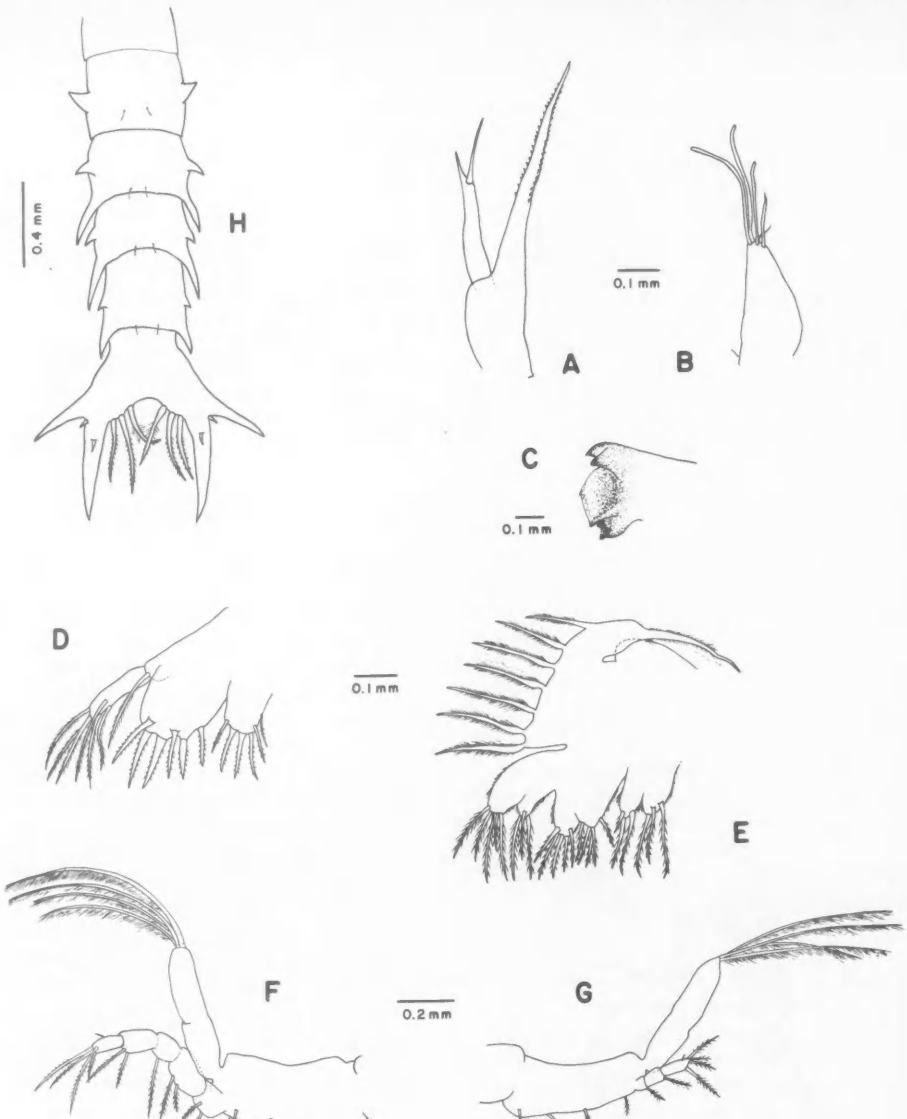

FIGURE 2.—*Geryon quinquedens*, Zoea I. A. antenna, B. antennule, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. dorsal view of abdomen and telson.

five-segmented with 2, 2, 1, 2, 5 setae on the segments (proximally to distally); basipodite with 10 setae, coxa with 1 seta. The exopodite of the second maxilliped (Figure 2G) bears four, one-jointed natatory setae terminally; endopodite three-segmented with 1, 1, 5 setae; basipodite with four setae; coxa naked.

ZOEA II (Figure 1B)

Carapace length 1.07 mm (1.00-1.13), total length 4.97 mm (4.89-5.02). Spines on carapace as in Zoea I. The rostral spine is nearly as long as the dorsal spine. Width of carapace from tip to tip of lateral spines about four-tenths the total length of the body. A short, slender seta is present at each side of the posterior margin of the dorsal spine's base. One to four small setae are scattered along the anterior edge of the proximal half of the dorsal spine; a small seta is present slightly above and in line with the base of each eye. Eyes stalked. Posteroventral edge of carapace finely serrate with three of four short, slender setae on the inner margin. Abdomen with five free somites (sixth fused with telson) (Figure 3H). Spination and setation as in Zoea I except an additional pair of short setae has been added proximally on the inner margin of the telson. The spines on the abdomen are somewhat more pronounced than in Zoea I. The antennule (Figure 3A) bears four aesthetes, plus one short and one long setae terminally. Protopodite of the antenna (Figure 3B) as in Zoea I; the exopodite terminates in two unequal setae and the endopodite is evident as a bud. Mandible as in Figure 3C. Endopodite of the maxillule (Figure 3D) as in Zoea I; a single, long plumose seta is present on the protopodite; basal endite with 12 spinous setae, coxal endite with 11. The scaphognathite of the maxilla (Figure 3E) bears 22 marginal plumose setae; endopodite bilobed with five setae on the distal lobe, three on the proximal; basal endite with seven setae on the distal lobe, five on proximal; coxal endite with four setae on each lobe. The two-segmented exopodite of the first maxilliped (Figure 3F) now bears 10 or 11 articulated natatory setae terminally; endopodite, basipodite, and coxa as in Zoea I. The exopodite of the second maxilliped (Figure 3G) bears 11 articulated natatory setae; endopodite, basipodite, and coxa as in Zoea I. The third maxillipeds, chelipeds, and pereiopods are evident as minute buds.

ZOEA III (Figure 1C)

Carapace length 1.42 mm (1.35-1.48); total length 6.13 mm (5.75-6.48). The lateral spines are more ventrally flexed and the number of small setae on the anterior edge of the dorsal spine has increased from the previous stage. There are 15 small setae along the inner margin of each side of the posteroventral and posterior edge of the carapace. Abdomen with six somites and the telson (Figure 4I). The spination and setation of somites two through five is the same as in the previous stage. The first somite now bears two small setae on the middorsal surface; sixth segment naked. Telson with five pairs of setae on the inner portion. The pleopods are evident as buds on somites 2 through 5; uropods as buds on the sixth. Antennule (Figure 4A) with four aesthetes and three setae terminally, plus three aesthetes subterminally; basal portion swollen and the endopod occurs as a small bud. The protopodite and exopodite of the antenna (Figure 4B) as in the previous stage; the endopodite is now about the same length as the exopodite. The mandible (Figure 4C) now bears a simple palp, evident as a bud. The endopodite of the maxillule (Figure 4D) has five or six long plumose setae on the distal segments; the basal and coxal endites each bear about 17 spinous setae. The scaphognathite of the maxilla (Figure 4E) bears about 31 marginal plumose setae; endopodite and basal endite as in previous stage; coxal endite with five spinous setae on distal lobe, and nine on the proximal lobe. The exopodite of the first maxilliped (Figure 4F) bears about 14 articulated natatory setae terminally; the distal segment of the endopodite now bears six setae; setation of other segments as in the previous stages, as is that of the basipodite; coxa with three setae. The exopodite of the second maxilliped (Figure 4G) bears about 14 articulated natatory setae; setation of endopodital segments as in the previous stages; basipodite with

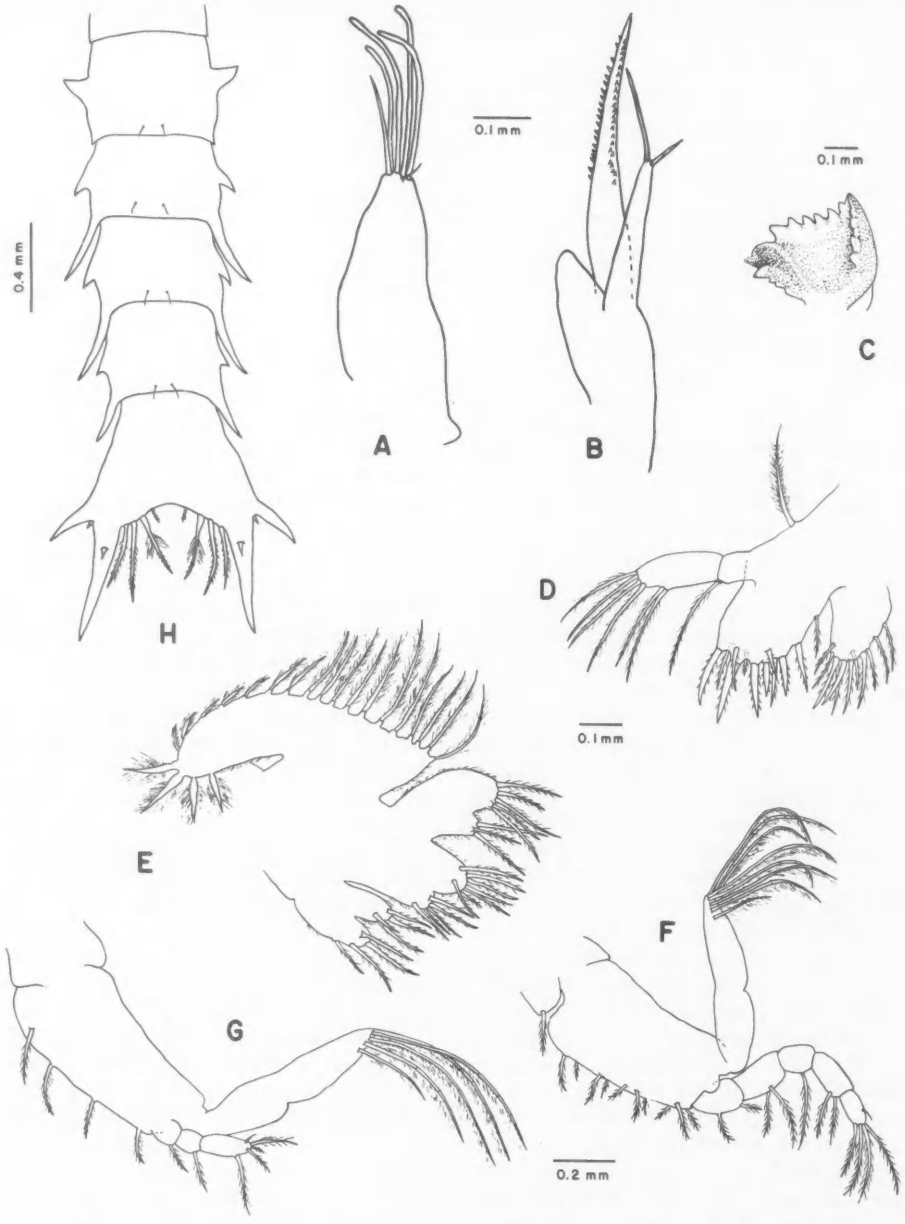

FIGURE 3.—*Geryon quinquedens*, Zoea II. A. antennule, B. antenna, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. dorsal view of abdomen and telson.

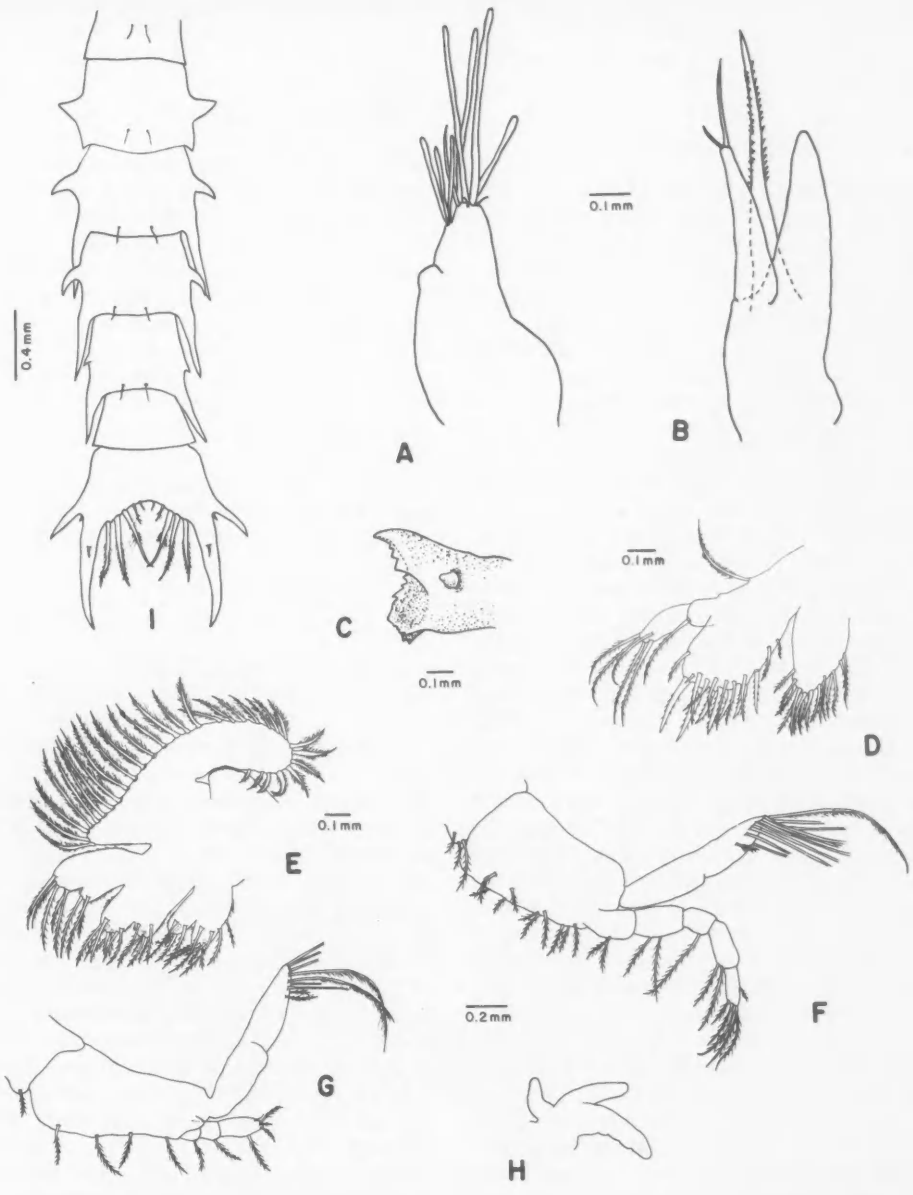

FIGURE 4.—*Geryon quinquedens*, Zoea III. A. antennule, B. antenna, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. third maxilliped, I. dorsal view of abdomen and telson.

three or four setae; coxa with one seta. The rudimentary third maxilliped as in Figure 4H. Chelipeds and pereiopods about twice as large as in previous stage.

ZOEA IV (Figure 1D)

Carapace length 1.94 mm (1.89-1.97); total length 8.31 mm (7.62-8.95). There is an indication that the considerable range in total and dorsal spine length is due to the nearness of a particular animal to its next molt. In some individuals a relatively short, blunt dorsal spine was observed; these individuals showed the greatest total length, while on shorter individuals a relatively long, slender dorsal spine was observed. Dorsal spine from 20 to 30% of the total length, with small setae scattered along its entire anterior edge; rostral spine usually as long or longer than the dorsal spine. Lateral spines flexed ventrally; carapace width, from tip to tip of lateral spines, about one-third of the total length of the body. A few additional setae occur between the anterior edge of the dorsal spine and the base of the rostral spine; 20 to 25 slender setae mid-ventrally to posteriorly on the inner margin of the carapace. Abdomen with six somites and the telson (Figure 5I). The blunt lateral spines on the second somite now directed slightly posteriad; spines on other somites more pronounced than in the previous stage. The first somite bears four setae on the middorsal surface; the second somite with two setae anterior and four setae posterior to the midline; the third somite with two setae middorsally and two on the posterodorsal margin; somites 4 and 5 each with a pair of setae on the posterodorsal margin, sixth somite naked; telson as in previous stage but with the proximal setae on the inner portion larger; pleopods and uropods considerably enlarged from the previous stage. Antennule (Figure 5A) with four aesthetes and two setae terminally, one group of six aesthetes and another of two subterminally; bud of endopod enlarged from previous stage; basal portion with five setae. Antenna (Figure 5B) as in previous stage but with the endopodite considerably enlarged and longer than the protopodite. Mandibular palp (Figure 5C) simple and much enlarged from the previous stage. The endopodite of the maxillule (Figure 5D) the same as in the previous stages; basal endite with about 22 spinous setae, coxal endite with 17. Scaphognathite of the maxilla (Figure 5E) with about 54 marginal plumose setae; endopodite the same as in the previous stages; distal lobe of the basal endite with 12 spinous setae, proximal lobe with nine; coxal endite as in the previous stage. The exopodite of the first maxilliped (Figure 5F) bears 17 setae; endopodite and basipodite as in the previous stage; coxa with six setae. The exopodite of the second maxilliped (Figure 5G) with 19 setae; the terminal segment of the endopodite with six setae, other segments as in the previous stages; basipodite with three setae; coxa with one. Exopodite of the third maxilliped (Figure 5H) with slight articulation; endopodite faintly five-segmented, the two distal segments each with one spine. Chelipeds and pereiopods considerably enlarged from previous stage.

MEGALOPA (Figures 6A and 7A)

Carapace length 3.16 mm (3.02-3.26); total length 6.46 mm (6.32-6.60). Rostrum one-fifth the length of the carapace, strongly depressed and bifid at the tip; a medial groove present from interorbital position nearly to the distal end of the rostrum. Eye stalks with a few small setae on the anterior and dorsal surfaces. A carina is present on each side of the mesogastric midline (highest points on carapace) and another prominence is present in the cardiac region of the carapace; hepatic and branchial lobes rounded; setation sparse, occurring along the margins of the rostrum, a few in the postorbital region, and a few tufts on the mesogastric prominences; numerous setae are present along the mid-ventral to posterior margin of the carapace. Abdomen with six somites and the telson; setation sparse and as figured; pleopods with about 28 long natatory setae each (Figure 7D); uropods with about 15 each (Figure 7H). The peduncle of the antennule (Figure 6B) is three-segmented, the proximal segment with one plumose seta, the middle segment with five setae subterminally, and the distal segment has two setae; inner

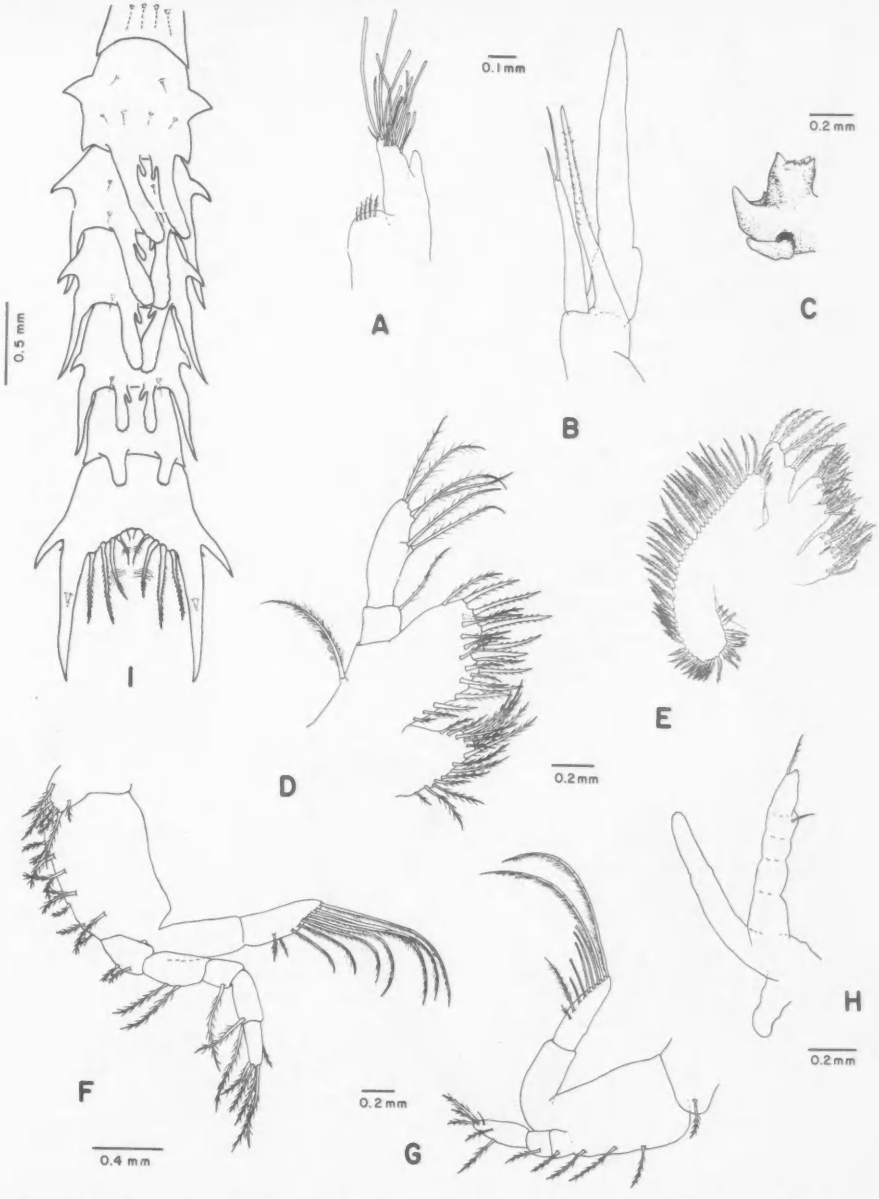

FIGURE 5.—*Geryon quinquedens*, Zoea IV. A. antennule, B. antenna, C. mandible, D. maxillule, E. maxilla, F. first maxilliped, G. second maxilliped, H. third maxilliped, I. ventral view of abdomen and telson.

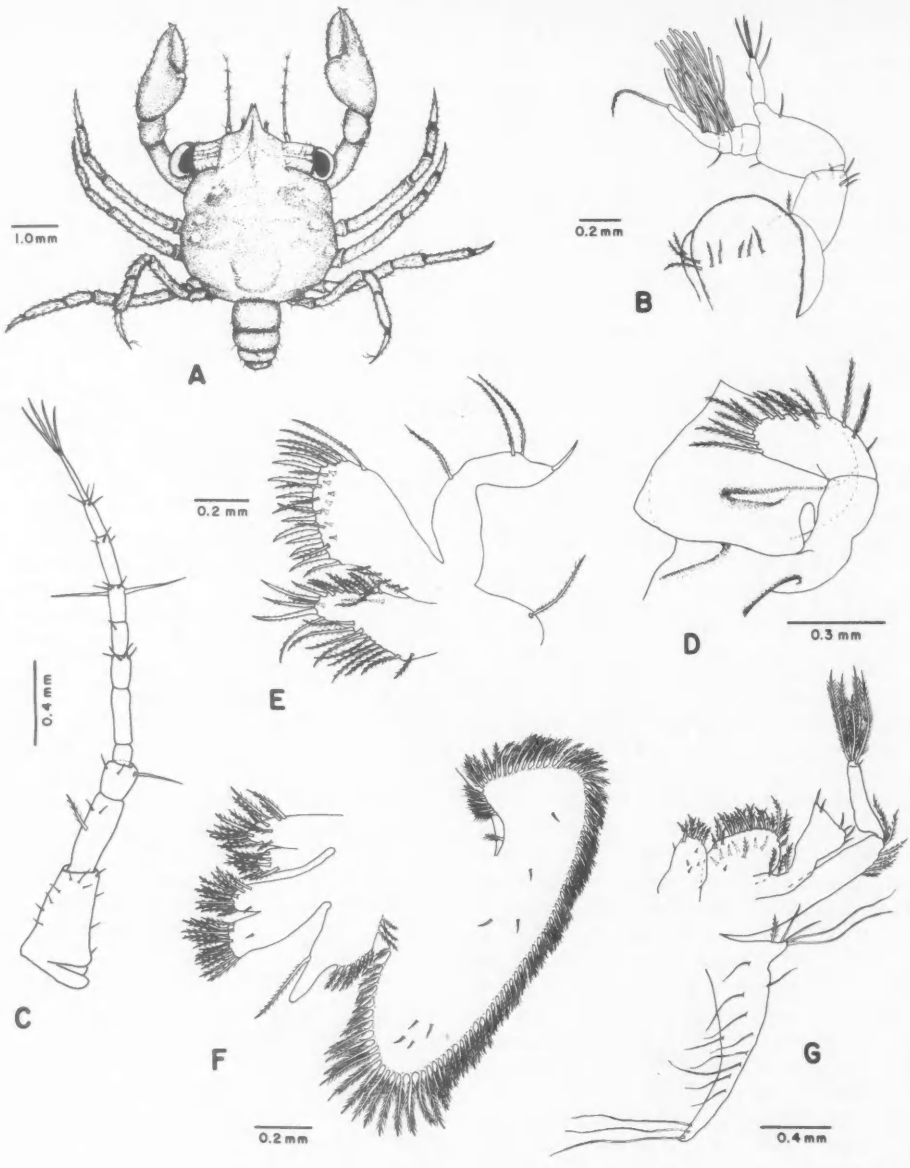

FIGURE 6.—*Geryon quinquedens*, megalopa. A. dorsal view, B. antennule, C. antenna, D. mandible, E. maxillule, F. maxilla, G. first maxilliped.

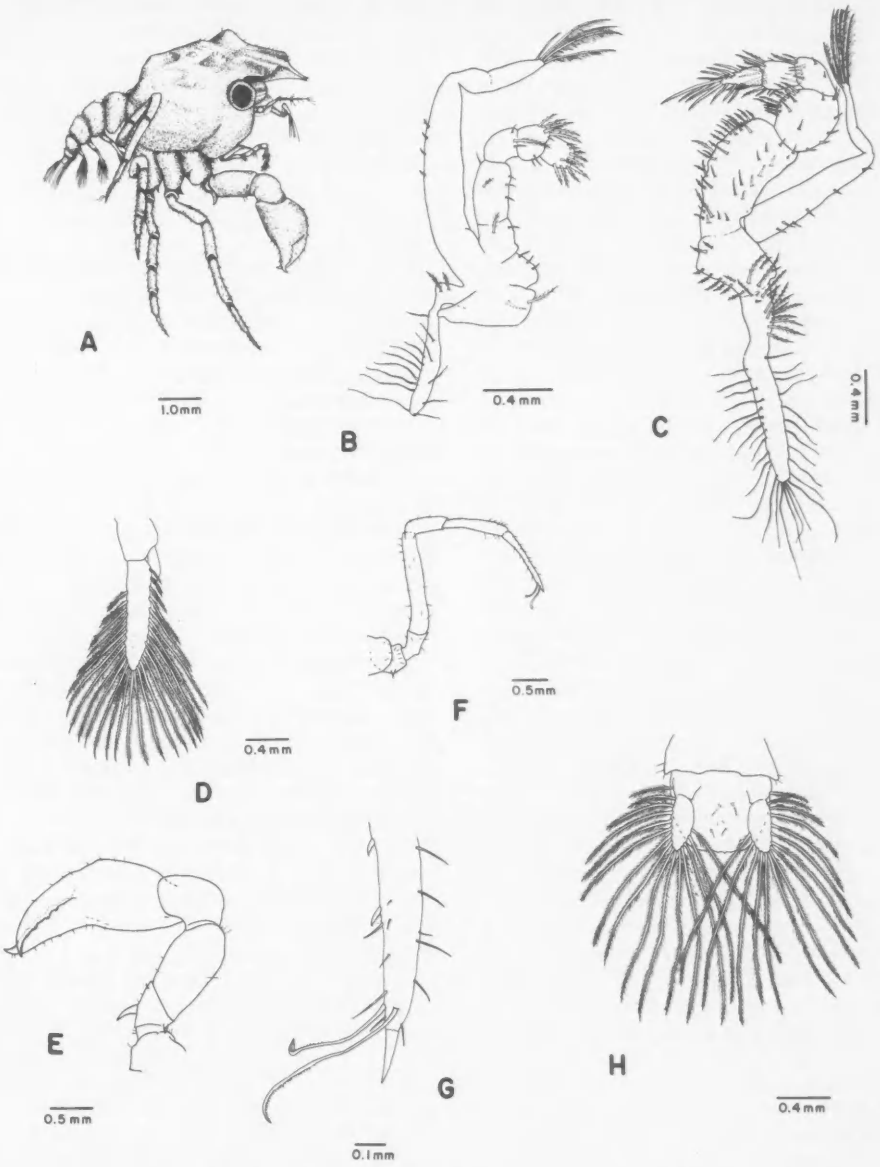

FIGURE 7.—*Geryon quinquedens*, megalopa. A. lateral view, B. second maxilliped, C. third maxilliped, D. pleopod of second abdominal somite, E. cheliped, F. last pereiopod, G. dactyl of last pereiopod, H. ventral view of telson and uropods.

flagellum two-segmented with four setae terminally and two subterminally; outer flagellum with four segments; proximal segment naked, the antepenultimate segments with six aesthetes, penultimate with five aesthetes and one seta, distal segment with five aesthetes near its base and one seta subterminally, terminating in a long, plumose seta. The basal portion of the antenna (Figure 6C) is two-segmented with small setae scattered on the distal segment; peduncle two-segmented with three setae on each segment; the flagellum is eight-segmented, the setation as figured. Mandibular palp two-segmented with 16 setae on the distal segment (Figure 6D). The endopodite of the maxillule (Figure 6E) is unsegmented, has one lateral and two subterminal setae, and terminates in a spine; the basal endite bears about 35 spinous setae; the coxal endite with about 25. The scaphognathite of the maxilla (Figure 6F) with about 100 marginal plumose setae, with a few setae scattered on the dorsal and ventral surfaces; endopodite produced into a narrow lobe, with three setae on the distal margin of the base, eight setae laterally on the same margin, and one long setae on the proximate lateral edge; basal endite with about 14 spinous setae on the distal lobe, 11 on the proximal; coxal endite with eight spinous setae on the distal lobe and 16 on the proximal. The exopodite of the first maxilliped (Figure 6G) now terminates in but five plumose setae and one naked seta; the endopodite is unsegmented and bladelike; basal endite with about 37 spinous setae along the margin; coxal endite with 12; epipodite with about 16 nonplumose hairs and 1 seta; setation of other portions as figured. A well-developed epipodite is present on the second maxilliped (Figure 7B) and bears about 14 nonplumose hairs and 2 setae; the exopodite terminates in four plumose and one nonplumose setae, and there are four short setae on the outer lateral margin; the endopodite with four segments, the distal segment with about 13 spinous setae terminally; other setation as figured. The exopodite of the third maxilliped (Figure 7C) terminates in six plumose setae; the endopodite is five-segmented, its spination and setation variable as is that of the epipodite and is approximately as figured. Chelipeds (Figure 7E) with a strong hooked spine on ventral portion of ischum. Spines on coxa of pereiopods one through three and another blunt spine subterminally on the posterior margin of the same articulation, decreasing in size posteriorly. Dactyl of last pereiopod with two curved, toothed setae (Figure 7F and G).

DISCUSSION

The prezoea and first zoea stages of *Geryon quinquedens* appear to be quite similar in structure to the corresponding stages of *G. tridens* described by Brattegard and Sankarankutty (1967). The most trenchant differences are the larger size of the zoea of *G. quinquedens* and the lack of posterolateral spines on the fifth abdominal somite in *G. tridens*. Brattegard and Sankarankutty give the length of the first zoea as 2.0 mm but no mention is made as to how they arrived at this measurement. The large size of the larvae of *G. quinquedens* should help to distinguish them from other sympatric Brachyrhyncha, with the possible exception of its congener, *G. affinis*.

The family Geryonidae was erected in 1930 by Beurlen (original reference not obtained, information from Christiansen, 1969), but since then *Geryon* has been placed in various families: Rathbun (1937) places *Geryon quinquedens* in the subfamily Carcinoplacinae of the family Goneplacidae; Bouvier (1940) placed *Geryon* in the family Xanthidae; Gurney (1939) lists the genus under the subfamily Menippinae of the family Xanthidae; and more recently Christiansen (1969) reassigned the genus to the family Geryonidae.

I have found few references dealing with the larvae of goneplacid genera. Lebour (1928) discussed the larval stages of *Gonoplax rhomboides;* Kurata (1968) described the larvae of *Carcinoplax longimanus*. Both of these species agree generally with *Geryon* in the number of larval stages, the spination of the carapace and abdomen, and the spination and setation of the telson. The relative length of the exopodite to the protopodite of the antenna in *Geryon* is apparently similar to that in *Carcinoplax* but different from that in *Gonoplax*. Megalopa of both *Gonoplax*

and *Carcinoplax* bear spines on the carapace, while megalopa of *Geryon* do not.

The exopodite of the antenna in zoeae of *Geryon quinquedens* is about one-half the length of the protopodite; in *Gonoplax* (Lebour, 1928) the exopodite is about the same length as the protopodite, and bears two short setae medially, rather than terminally as in *Geryon*. On the basis of the relative length of these two structures, *Geryon* would not align with *Gonoplax* in Lebour's key to the zoeae. The configuration and relative length of the antennal exopodite and protopodite in *Geryon* are more like those of *Cancer* (Poole, 1966), some portunids (Lebour, 1928; Roberts, 1969) and certain grapsids (Diaz and Ewald, 1968). Boyden (1943) and Leone (1951) discuss the serological relationships of *Geryon quinquedens* to other members of the Brachyura. Each found *Geryon* to be closer to the Xanthidae than to other families tested, with certain affinities noted to the Cancridae and Portunidae. However, neither of these workers tested other members of the Goneplacidae against *Geryon*. The zoeae of *Geryon quinquedens* are similar to most xanthid zoeae (Lebour, 1928; Costlow and Bookhout, 1968) in the number of zoeal stages, the spines on the carapace, and the armature of the telson. However, there are differences in the latter two characters within the Xanthidae alone (Costlow and Bookhout, 1966). The structure of the zoeal antennae of *Geryon* is decidedly different from the antennae of xanthid zoeae; in xanthid zoeae the exopodite of the antenna is very short in relation to the length of protopodite.

The number of terminal setae on the exopodite of the first and second maxillipeds of Zoea II through IV apparently distinguish the larvae of *Geryon quinquedens* from other members of the Brachyrhyncha. In this group the exopodite of the first maxillipeds consistently bear four terminal setae in the first zoeal stage and six in the second stage. The same number is usually associated with the second maxilliped. *G. quinquedens* bears 4 setae in the first stage and 10 or 11 in the second. Knight (1968) reports that the raninid species, *Raninoides benedicti* Rathbun, has nine setae on the exopodite of the second maxilliped (six on the first) of Zoea II. Only members of the rather diverse and remote Anomura apparently bear as many terminal setae on the maxillipeds of stages subsequent to Zoea I as does *G. quinquedens*. The lithodid species, *Cryptolithodes typicus* Brandt, bears four setae on the exopodite of the first maxilliped in the first zoeal stage and eight in the second stage (Hart, 1965). The porcellanid genera *Polyonyx* (Knight, 1966; Gore, 1968), *Pachycheles*, and *Petrolisthes* (Greenwood, 1965) bear from 11 to 14 terminal setae on the exopodite of the first maxillipeds in Zoea II. All bear four setae on this structure in Zoea I.

ACKNOWLEDGMENTS

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THE SYSTEMATIC STATUS OF *MERLUCCIUS* IN THE TROPICAL WESTERN ATLANTIC OCEAN INCLUDING THE GULF OF MEXICO

CHARLES KARNELLA[1]

ABSTRACT

Several morphometric and meristic characters are used to compare populations of *Merluccius* from the Gulf of Mexico and Atlantic Ocean. Both populations are shown to have similar values for all characters studied. As a result *M. magnoculus* Ginsburg is relegated to the synonymy of *M. albidus* (Mitchill).

Geographical variation is noted in many of the characters investigated.

The widely distributed gadoid fish genus *Merluccius* contains an indeterminate number of commercially fished species. There are 11 nominal species (Grinols and Tillman, 1970), known variously in the United States as either whiting or hake. The object of this paper is to determine the number of species living in the tropical western Atlantic (including the Gulf of Mexico and Caribbean). Ginsburg (1954) recognized three species from the western North Atlantic. One of these, *M. bilinearis* (Mitchill), is distinct from the other two nominal forms in having more gill rakers on the first arch (15-22 vs. 9-12). This species will not be considered further as it does not occur south of Cape Fear, N.C. *M. magnoculus* Ginsburg was described as new mainly on the basis of its having a longer head and shorter paired fins than its closest relative, *M. albidus* (Mitchill). *M. albidus* is found in the tropical western Atlantic, although not exclusively so, as it is known to occur sympatrically with *M. bilinearis* in the north. Ginsburg further noted that *M. magnoculus* and *M. albidus* were also moderately to slightly divergent in the following characters: maxillary length, snout length, eye diameter, and number of first dorsal, second dorsal, pectoral, and anal fin rays. Moreover, *M. magnoculus* was confined to the Gulf of Mexico while *M. albidus* occurred off the eastern coast of North America from Georges Bank to the Tortugas off the west coast of Florida. The lack of comparative material of equivalent size from the Gulf, the doubtful systematic status of two specimens from Savannah, Ga., and of a single specimen from off Cape Canaveral, Fla., make uncertain Ginsburg's tentative assignation of these specimens to *M. albidus*. Difficulty in identifying subsequent material from the Gulf of Mexico and Caribbean has necessitated a reassessment of the taxonomic status of *M. albidus* and *M. magnoculus*, especially since the stated differences between the two are slight and there is at least some overlap in all characters used to separate them.

Throughout the body of this paper the Atlantic population is taken to include specimens from the Caribbean also.

MATERIAL

A total of 253 specimens was examined; 86 from the Gulf of Mexico and 167 from along the eastern coast of the Americas, lat 41°30′N south to lat 7°26′N (Figure 1). This total included Ginsburg's material whenever possible. How-

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ever, some of his specimens were in poor state of preservation and too fragile to be handled. The list of specimens is as follows:

ATLANTIC OCEAN AND CARIBBEAN SEA

U.S. National Museum (USNM): 25769-1 specimen; 26049-1; 26073-1; 31630-1; 31677-1; 31686-1; 31739-1; 31741-1; 31822-1; 31842-2; 31844-1; 31863-2; 32791-1; 33032-1; 44264-1; 45920-1; 155475-2; 159214-1; 159230-1; 186294-5; 186299-1; 186302-1; 190356-1; 205223-1; 205224-1; 205230-1; 205231-1; 205233-1; 205235-1; 205237-4; 205240-2; 205241-1; 205242-1; 205243-1; 205244-1; 205245-1; 205246-1; 250247-1; 205248-1; 205249-1; 205251-1; 205252-1; 205253-1; 205255-1; 205257-2; 205259-1; 205260-1; 205262-1; 205263-2; 206190-1; 206191-1; 206192-2; 206194-1; 206195-7; 206196-1; 206197-1; 206198-1; 206199-1; 206200-1; 206201-2; 206202-5; 206203-4; 206204-1; 206205-30; 206207-2; 206208-5; 207187-3; 207188-1; 207189-1.

University of Miami Marine Laboratory (UMML): 3418-2 specimens; 3696-2; 4431-2; 22957-2; 29224-5; 29506-4; 29508-1.

Museum of Comparative Zoology (MCZ): 37754-2 specimens; 38086-3; 38130-3; 38324-1; 38333-1; 38338-2; 38350-1; 38395-1; 38399-2.

GULF OF MEXICO

U.S. National Museum (USNM): 92045-2 specimens; 157757-1; 157758-2; 157759-5; 157760-5; 157761-4; 157762-2; 157763-10; 186331-2; 187134-5; 187136-1; 205225-1; 205226-1; 205227-2; 205228-1; 205229-3; 205232-3; 205234-2; 205236-1; 205238-1; 205239-1; 205250-1; 205254-3; 205256-1; 205258-1; 205261-1; 206187-1; 206188-2; 206189-2; 206193-4; 206206-3; 207153-2; 207190-1.

University of Miami Marine Laboratory (UMML): 29507-9 specimens.

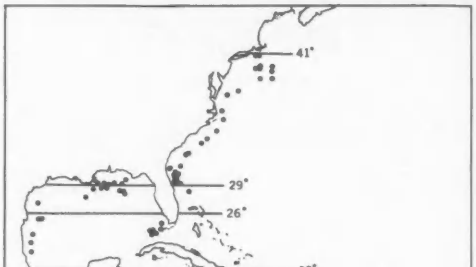

FIGURE 1.—Distribution of samples, western North Atlantic Ocean; equator to lat 45°N.

METHODS

All counts and measurements were made as described in Ginsburg (1954), so that the data from both studies would be directly comparable. The median fin rays, except the caudal, pectoral rays on both sides, and gill rakers of the outer arch on both sides were counted on all specimens that were not damaged. Total vertebral counts were made on selected specimens. Standard length, head length, snout length, maxillary length, eye diameter, pectoral fin length, and pelvic fin length were measured on all specimens when possible.

RESULTS AND DISCUSSION

Inspection of the counts and measurements indicates that the Gulf and Atlantic populations are similar in all characters studied. Within each area there are local differences in most of the characters; however, these differences are minor. The Gulf and Atlantic populations have identical or nearly identical ranges for all characters investigated, and the average values for both are generally only slightly divergent.

Differences in the relative head length and the

relative length of the paired fins were the main criteria used by Ginsburg (1954) for recognizing the Gulf population as a distinct species, *M. magnoculus*. These differences, however, were minor. More importantly the material used in his study did not adequately represent either the Atlantic or Gulf population. Thirty of thirty-eight specimens from the Atlantic were taken off Long Island, N.Y., and all 32 of the specimens from the Gulf of Mexico came from north of lat 26°N. Ginsburg was not able to make a valid comparison of the Atlantic and Gulf populations with the limited material available to him.

HEAD LENGTH

Ginsburg (1954) listed the range of head length taken as a percent of standard length as 27.3-31.3 for *M. albidus* and 29.6-31.3 for *M. magnoculus* but gave no mean values. Average values calculated from the data in Table 8 in Ginsburg (1954) are 28.7 for *M. albidus* and 30.6 for *M. magnoculus*. The specimens from the Atlantic and Caribbean populations examined in this study, had a range of 26.4-32.9 and a mean of 29.0, while the Gulf population had a range of 27.3-31.3 with a mean of 29.7. As can be seen from Table 1 the head length expressed as a percent of standard length is fairly uniform over the entire geographic area represented in this study.

TABLE 1.—Head length as a percent of standard length for the Atlantic and Gulf populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	27.9-31.8	29.8
21°-41°N	114	26.4-32.9	28.7
7°-41°N	162	26.4-32.9	29.0
Gulf			
19°-25°N	42	27.3-31.2	29.4
26°-29°N	43	28.6-31.3	30.0
19°-29°N	85	27.3-31.3	29.7

Although the Gulf population does have a slightly larger head, degree of difference between the two populations reported by Ginsburg is unsupported by the present data. The two populations are not separable on the basis of relative length.

Ginsburg also stated that growth of the head was allometric. The present data indicate that growth of the head is isometric (see Figure 2).

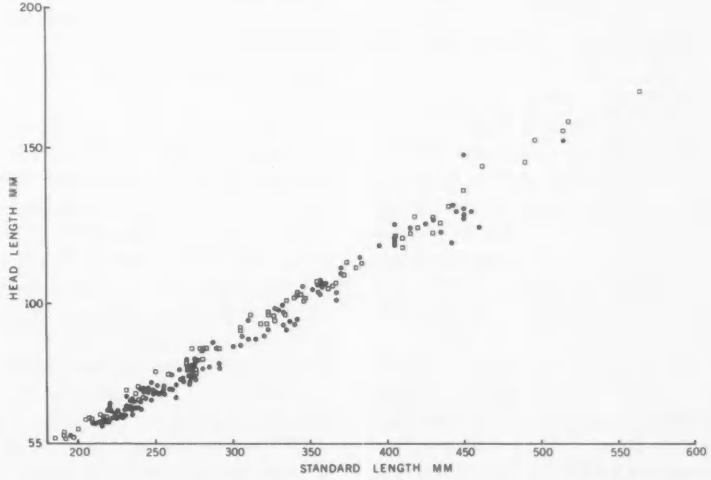

FIGURE 2.—Gulf (squares) and Atlantic (circles) populations: relation of head length to standard length.

PAIRED FIN LENGTH

Ginsburg (1954) reported the range of pectoral fin length taken as a percent of standard length to be 18.0-21.5 and 15.5-19.0 for *M. albidus* and *M. magnoculus*, respectively. The Atlantic specimens examined in the study have a similar maximum value to that of *M. albidus* (21.7, see Table 2) but the minimum value obtained, 13.7, is much lower. The minimum value obtained from the Gulf population, 13.7, is somewhat lower than the minimum value recorded for *M. magnoculus*, while the maximum value obtained, 19.4, is similar to that given by Ginsburg for *M. magnoculus*. Average values calculated from the data in Table 10 in Ginsburg (1954) are 19.8 for *M. albidus* and 17.0 for *M. magnoculus*. These compare fairly well with the values obtained for the Atlantic and Gulf populations 18.3 and 16.8, respectively.

TABLE 2.—Pectoral fin length as a percent of standard length for the Atlantic and Gulf populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	13.7-19.5	17.3
21°-41°N	113	15.8-21.7	18.8
7°-41°N	161	13.7-21.7	18.3
Gulf			
19°-25°N	41	13.7-19.2	17.2
26°-29°N	42	13.8-19.4	16.4
19°-29°N	83	13.7-19.4	16.8

The range of values for the pelvic fin length expressed as a percent of standard length is 12.8-19.2 with an average value of 15.6 for the Atlantic population and 11.6-17.0 with a mean of 14.3 for the Gulf population (Table 3). Ginsburg also reported a range of 13.5-19.5 for *M. albidus* and 12.0-16.0 for *M. magnoculus*, and the averages computed from data contained in his Table 9 are 16.6 and 14.0 for *M. albidus* and *M. magnoculus*, respectively.

The present data indicate that the Gulf population does have proportionally smaller paired fins than the Atlantic population, however, the differences are much smaller than indicated by Ginsburg. The relative length of the paired fins is similar in both populations and is clearly of no value in separating the two.

TABLE 3.—Pelvic fin length as a percent of standard length for the Gulf and Atlantic populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	12.8-19.2	14.7
21°-41°N	114	12.8-17.7	15.9
7°-41°N	162	12.8-19.2	15.6
Gulf			
19°-25°N	41	12.7-17.0	15.1
26°-29°N	43	11.6-16.2	13.6
19°-29°N	84	11.6-17.0	14.3

Ginsburg (1954) stated that the growth of the pelvic fin was allometric and that the relative pectoral fin length changed little if any with growth. To compensate for this he arranged his material into several size classes and compared similar sizes for both populations. However, he gave no average standard length for the classes, and it is impossible to determine if the size composition of the classes he compared was similar. Figure 3 indicates that growth of the pectoral fin is allometric and not isometric as reported by Ginsburg (1954). The pelvic fin does undergo allometric growth as stated by Ginsburg (see Figure 4).

Since the material examined from both areas is not of the same size composition (the average standard length of the specimens from the Atlantic population is 283 mm while the average standard length of the specimens from the Gulf population is 323 mm) at least some of the difference in paired fin length is due to allometric growth.

Figures 3 and 4 indicate that for some of the Gulf material the paired fins are relatively smaller than in other specimens of similar sizes. The majority of specimens with the smaller fins were collected north of lat 26°N. Most of the specimens with the higher values were collected north of lat 21°N in the Atlantic. Many specimens examined from the northern Gulf have fins of the same size as specimens from the southern Gulf and Atlantic populations. Hence, not all of the northern Gulf material can be distinguished by relative fin size.

The paired fins are poor characters to use in *Merluccius* because they are generally damaged to some degree. It is often impossible to determine if the fine ends of the rays are broken off.

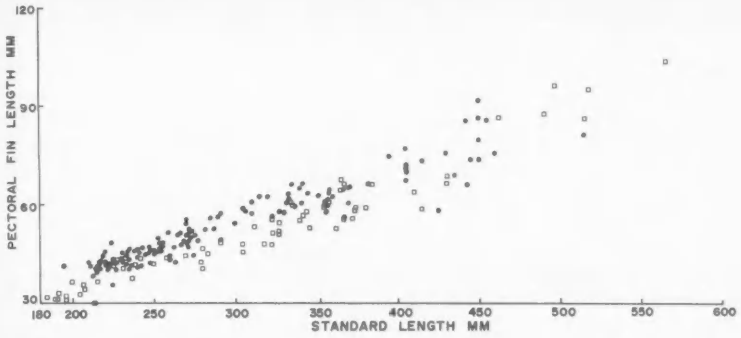

FIGURE 3.—Gulf (squares) and Atlantic (circles) populations: relation of pectoral fin length to standard length.

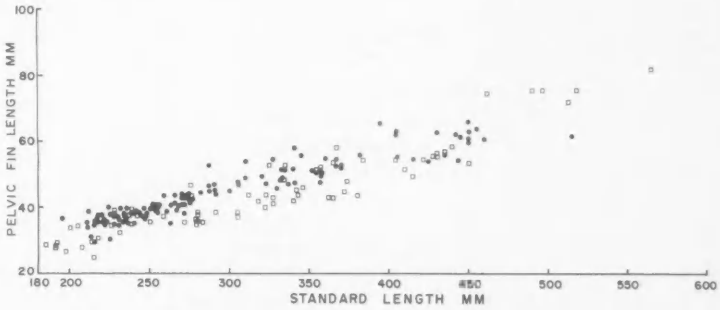

FIGURE 4.—Gulf (squares) and Atlantic (circles) populations: relation of pelvic fin length to a standard length.

Although the proportion and degree of damaged fins should be the same for both populations, a slight error will be introduced, and values presented for these measurements should be considered only as approximations of the real values.

EYE DIAMETER, SNOUT LENGTH, AND MAXILLARY LENGTH

The values obtained for these characters were similar in the Atlantic and Gulf populations, with the Gulf population having a slightly larger average value for all three characters (Tables 4, 5, 6); these values agree well with those of Ginsburg (1954).

All differences in these characters reported by Ginsburg (1954) may be explained by his limited material. Material from other areas examined in the present investigation indicate there are no differences between the two populations in any of the above characters (Figures 5, 6, 7).

TABLE 4.—Eye diameter as a percent of standard length for the Gulf and Atlantic populations.

Population	*N*	Range	Mean
Atlantic			
7°-20°N	48	4.6-8.4	5.6
21°-41°N	114	4.8-8.4	5.9
7°-41°N	162	4.6-8.4	5.9
Gulf			
19°-25°N	42	5.2-7.0	6.0
26°-29°N	43	4.8-7.1	6.1
19°-29°N	85	4.8-7.1	6.0

TABLE 5.—Snout length as a percent of standard length for the Gulf and Atlantic populations.

Population	N	Range	Mean
Atlantic			
7°-20°N	44	8.8-10.7	9.7
21°-41°N	114	8.1-11.1	9.2
7°-41°N	158	8.1-11.1	9.4
Gulf			
19°-25°N	42	8.7-11.2	9.8
26°-29°N	43	9.2-10.8	10.2
19°-29°N	85	8.7-11.2	10.0

TABLE 6.—Maxillary length as a percent of standard length for the Gulf and Atlantic populations.

Population	N	Range	Mean
Atlantic			
7°-20°N	48	13.6-16.8	15.0
21°-41°N	114	13.3-17.7	14.4
7°-41°N	162	13.3-17.7	14.6
Gulf			
19°-25°N	42	13.6-15.9	15.0
26°-29°N	43	14.7-16.2	15.3
19°-29°N	85	13.6-16.2	15.2

Eye diameter is quite variable and several workers have noted that there are big eyed and small eyed forms in the Caribbean and Gulf of Mexico (D. M. Cohen, National Systematics Laboratory, National Marine Fisheries Service, NOAA, Washington, DC 20560, pers. comm.). Figure 5 indicates that the eye size is quite variable and there is no division between the big eyed and small eyed forms.

Eye size does not appear to be related to sex. Females (73 specimens) with small, intermediate, and large eyes were noted. Only two males were found, both with eyes of intermediate size.

MERISTIC CHARACTERS

Values obtained for meristic characters (Tables 7, 8, 9, 10, 11) are in agreement with those given by Ginsburg (1954) for both pop-

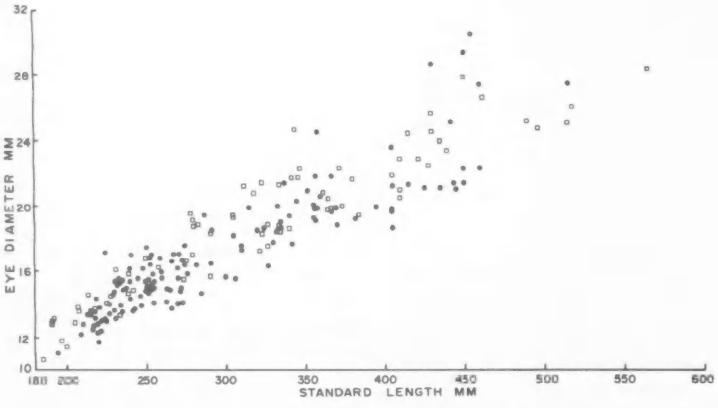

FIGURE 5.—Gulf (squares) and Atlantic (circles) populations: relation of eye diameter to standard length.

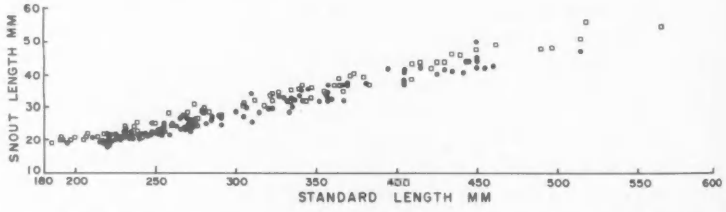

FIGURE 6.—Gulf (squares) and Atlantic (circles) populations: relation of snout length to standard length.

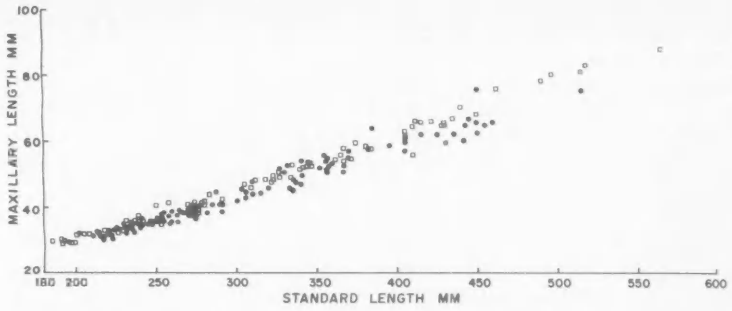

FIGURE 7.—Gulf (squares) and Atlantic (circles) populations: relation of maxillary length to standard length.

TABLE 7.—Frequency distribution of the number of gill rakers on the first gill arch for the Gulf and Atlantic populations.

Population	Number of gill rakers					
	8	9	10	11	12	Mean
Atlantic						
7°-20°N	3	22	46	24	3	10.0
21°-41°N	1	14	157	56	3	10.2
7°-41°N	4	36	203	80	6	10.1
Gulf						
19°-25°N	2	21	54	5	---	9.8
26°-29°N	4	13	63	8	---	9.9
19°-29°N	6	34	117	13	---	9.8

TABLE 8.—Frequency distribution of the number of first dorsal rays for the Gulf and Atlantic populations.

Population	Number of first dorsal rays				
	10	11	12	13	Mean
Atlantic					
7°-20°N	---	14	32	3	11.8
21°-41°N	3	63	49	1	11.4
7°-41°N	3	77	81	4	11.5
Gulf					
19°-25°N	---	16	24	2	11.7
26°-29°N	---	4	32	8	12.1
19°-29°N	---	20	56	10	11.9

ulations. However, for all characters but the number of first dorsal rays there was an increase in the range of one to three elements. In general, the average values computed from data presented in Ginsburg (1954) for *M. albidus* and *M. magnoculus* agree well with the average values calculated for the Atlantic and Gulf populations respectively.

Total vertebral counts for the Atlantic and Gulf populations were similar in both ranges and averages (Table 12). Geographic variation in most meristic characters is slight. Vertebral elements, pectoral fin rays, and anal fin rays are more variable than other meristic characters examined.

The ranges for all meristic characters studied are identical or nearly so for both the Gulf and Atlantic populations. For all characters there is a difference of less than one element in the average value between the two populations. Within each population there is variation in some or all of the meristic characters studied. The

TABLE 9.—Frequency distribution of the number of second dorsal rays for the Gulf and Atlantic populations.

Population	Number of second dorsal rays							
	35	36	37	38	39	40	41	Mean
Atlantic								
7°-20°N	2	14	20	8	3	---	---	36.9
21°-41°N	---	3	22	42	39	9	1	38.3
7°-41°N	2	17	42	50	42	9	1	37.9
Gulf								
19°-25°N	---	6	14	12	8	2	---	37.7
26°-29°N	---	2	10	12	14	5	1	38.3
19°-29°N	---	8	24	24	22	7	1	38.0

TABLE 10.—Frequency distribution of the number of anal rays for the Gulf and Atlantic populations.

Population	Number of anal rays								
	35	36	37	38	39	40	41	42	Mean
Atlantic									
7°-20°N	2	6	22	15	2	--	--	--	37.2
21°-41°N	1	8	42	32	28	2	2	--	37.8
7°-41°N	3	14	64	47	30	2	2	--	37.6
Gulf									
19°-25°N	2	9	12	7	6	4	2	--	37.6
26°-29°N	--	2	2	7	13	15	4	1	39.2
19°-29°N	2	11	14	14	19	19	6	1	38.4

TABLE 11.—Frequency distribution of the number of pectoral rays for the Gulf and Atlantic populations.

Population	Number of pectoral rays						
	12	13	14	15	16	17	Mean
Atlantic							
7°-20°N	6	24	57	6	2	--	13.7
21°-41°N	--	1	28	124	72	4	15.2
7°-41°N	6	25	85	130	74	4	14.8
Gulf							
19°-25°N	--	13	27	25	15	2	14.6
26°-29°N	6	42	28	11	--	--	13.5
19°-29°N	6	55	55	36	15	2	14.0

northern Gulf population has a slightly higher average value than the southern Gulf population for all meristic characters except pectoral fin rays and vertebrae. The southern Gulf has on the average a greater number of pectoral fin rays and vertebrae (Tables 7, 8, 9, 10, 11, 12). In the Atlantic the more southerly populations have fewer vertebrae, pectoral rays, second dorsal rays, and anal rays and more first dorsal rays than the northern populations.

Material collected between lat 7° and 20°N in the Atlantic has on the average between two and three (2.5) fewer vertebrae than the material collected north of lat 21°N. There is very little overlap in the range of vertebrae in the northern and southern Atlantic populations. Only 1 of 41 specimens from south of lat 20°N has more than 53 vertebrae and only 13 of 87 specimens north of lat 20°N have less than 54 vertebrae (Table 12). However, the relatively few specimens collected between lat 16° and 20°N may not be representative of the population residing there due to sampling error and hence, not represent the true range of vertebrae for that population.

CONCLUSIONS

The above data suggest that there is but a single species of *Merluccius* in the tropical western Atlantic, including the Caribbean and Gulf of Mexico. The Gulf population as a whole cannot be distinguished from the Atlantic population by means of any of the characters examined. For all of the characters examined differences between both populations are small. Within each area there are local differences in most of the characters; however, these differences are minor. The Gulf and Atlantic populations have identical

TABLE 12.—Frequency distribution of the number of vertebrae for the Gulf and Atlantic populations.

Population	Number of vertebrae							
	50	51	52	53	54	55	56	Mean
Atlantic								
7°-20°N	6	7	19	8	1	--	--	51.8
21°-41°N	--	--	--	13	41	31	2	54.3
7°-41°N	6	7	19	21	42	31	2	53.5
Gulf								
19°-25°N	--	1	5	14	10	2	1	53.3
26°-29°N	--	1	15	9	4	1	--	52.6
19°-29°N	--	2	20	23	14	3	1	53.0

or nearly identical ranges for all characters investigated, and the average values for both are generally only slightly divergent.

The northern Gulf population is, in many characters, divergent from the northern Atlantic population, which led Ginsburg (1954) to describe this population as a distinct species. However, the northern Gulf population is also somewhat divergent from the southern Gulf and Atlantic populations and, in both cases, the divergence is clearly not great enough to warrant recognition at the specific level. Furthermore, the amount of overlap in all characters is of such magnitude that individuals of the northern Gulf population cannot always be distinguished from individuals from other areas. Hence, *M. magnoculus* Ginsburg should be considered a junior synonym of *M. albidus* (Mitchill).

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REGIONAL DISTRIBUTION OF THYROID STIMULATING HORMONE ACTIVITY IN THE PITUITARY GLAND OF THE ATLANTIC STINGRAY, *DASYATIS SABINA*

RODNEY G. JACKSON AND MARTIN SAGE[1]

ABSTRACT

The possibility that the elasmobranch pituitary contains thyroid stimulating hormone (TSH) activity was investigated by measuring the increase in the release of thyroxine from thyroid glands of the Atlantic stingray, *Dasyatis sabina*, incubated with homogenates of various pituitary regions. The ventral lobe of the pars distalis contained most of the TSH activity, with lesser amounts in the neurointermediate lobe. Histological techniques were not sensitive enough to detect changes in the thyroid associated with the increase in thyroxine release. It is concluded that the elasmobranch pituitary contains TSH activity but its functional significance remains to be determined.

Few studies have been conducted to examine the functional relationship between the pituitary and the thyroid gland of elasmobranchs. Dodd and Goddard (unpublished but cited by Dent and Dodd, 1961) hypophysectomized adult dogfish, *Scyliorhinus caniculus*, but found no histological changes in the thyroid after 2 years, whereas Vivien (1964) found that after decapitation of *Scyliorhinus* embryos the thyroid failed to complete its differentiation. The latter result is, of course, open to several interpretations since decapitation removes more than the pituitary. Injection of homoplastic pituitary homogenates into *Scyliorhinus* resulted in histological signs of stimulation of the thyroid gland (Vivien, 1941; Olivereau, 1954). Unfortunately, histological methods of assessing thyroid activity are frequently both insensitive (Sage and Robins, 1970) and unreliable (Swift, 1960).

Ferguson, Dodd, Hunter, and Dodd (unpublished data summarized by Dodd et al. (1963)) using the McKenzie mouse assay found thyroid stimulating hormone (TSH) activity in all parts of the *S. caniculus* pituitary, most of it being in the ventral lobe. However, the highest activity found was much less than that found in the posterior lobe of the mouse pituitary, which presumably does not contain TSH. Their results could be interpreted as suggesting that the small amount of TSH activity found in the dogfish pituitary was of no significance. The interpretation of assays of lower vertebrate TSH on mammalian assay systems is further complicated by the probability of phylogenetic specificity of hormone action. It is known that teleost TSH is relatively inactive on the mammalian thyroid (Fontaine, 1969); similarly it is possible that if there is an elasmobranch TSH it may have low activity on mammalian tissues. In a recent review Gorbman (1969) states that "definite proof of a TSH-like principle in elasmobranch pituitaries remains to be provided." In an attempt to elucidate this problem we investigated the stimulatory effects of homogenates of the different regions of the pituitary of *Dasyatis sabina* on thyroxine release from the animal's own thyroid gland in vitro. This technique eliminates the problem of phylogenetic specificity, and, by measuring thyroxine release, avoids the problems of interpretation associated with histological assessment of thyroid activity.

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MATERIALS AND METHODS

ANIMALS

Dasyatis sabina (Lesueur) were collected in otter trawls. In the fall and winter stingrays are most abundant in the shallow waters in the Gulf of Mexico adjacent to Port Aransas, Tex. In late spring the stingrays migrate into the bays behind the line of barrier islands where they were caught during the summer (Sage et al., 1972).

INCUBATION TECHNIQUE

Animals were killed by cutting across the hind brain. The compact thyroid is located ventral to the anterior end of the ventral aorta. The thyroid was removed and divided into experimental and control halves, and further divided where necessary so that no piece of tissue was larger than 5 mg. Preliminary experiments indicated that the elasmobranch thyroid was slow in responding to stimulation. Thyroid tissue was therefore incubated for 3 days in 2 ml of elasmobranch saline (Nicoll and Bern, 1964). Antibiotics were added (Bakke et al., 1957) in order to inhibit bacterial growth which might result in the breakdown of the thyroxine released into the medium. The addition of antibiotics does not interfere with the ability of thyroid glands to respond to TSH (Bakke et al., 1957; Sage, 1968a). The incubation flasks were gassed with 95% oxygen and 5% carbon dioxide and shaken at 120 strokes/min at 30°C. This temperature is within the normal environmental range of *D. sabina*. Modification of the incubation medium by the addition of 0.5 mg/ml lactalbumin hydrolysate was found to increase control rates but reduce the variability of the response and was used in later experiments as described in the text.

Homogenates of whole pituitaries or various regions of the stingray pituitary were made in a glass homogenizer and added to the incubation media at a concentration of one pituitary gland or region per thyroid gland. The homogenates were added immediately prior to gassing and adding of the thyroid tissue.

THYROXINE ANALYSIS

At the end of the 3-day incubation period thyroid tissue was removed for histological examination, and the incubation media was centrifuged at 10,000 rcf for 10 min to remove cell debris. Incubations were then stored below 0°C until analyzed. Thyroxine was isolated by ion exchange chromatography (Galton and Pitt-Rivers, 1959). The catalytic effect of iodine in reducing ceric ions was used to quantify thyroxine iodine (Pileggi et al., 1961; Pileggi and Kessler, 1968). Oxford Laboratories' (San Mateo, Calif.) kit[2] of reagents was used in the determinations. The results were converted to rates of thyroxine release per unit thyroid weight per incubation, and the responses of treated halves of the gland were then expressed as a percentage of the matched control incubated halves. Additives to the incubation media were routinely analyzed but were invariably devoid of thyroxine.

HISTOLOGICAL METHODS

At the end of the incubation period, thyroid tissue was removed and fixed in mercuric formol (90 parts saturated mercuric chloride to 10 parts formaldehyde solution). Sections were cut in polyester wax and stained with hematoxylin and light green. The image of the thyroid follicles was projected onto a sheet of paper, and a planimeter was used to determine the percentage of the area of follicle occupied by epithelium.

Unstained thyroid sections were used for interferometric determinations of mass per unit area of the colloid (Bromage and Sage, 1968; Sage, 1968b). Such methods are very sensitive in detecting changes in thyroid activity in both teleosts (Bromage and Sage, 1968) and mammals (Sage and Robins, 1970).

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

A preliminary study was carried out to determine responsiveness of the thyroid to homogenates of the various regions of pituitary and to control material. The results (Table 1) indicated that the addition of large amounts of protein or protein hydrolysate resulted in a stimulation of the gland, thus suggesting an inadequate culture medium. The medium was therefore modified by the addition of 0.5 mg lactalbumin hydrolysate/ml, and the response to various regions of the pituitary reexamined (Table 2). TSH activity was greatest in the ventral lobe of the proximal pars distalis, but significant activity was also found in the neurointermediate lobe. The latter is not due to the presence of thyroxine in this pituitary lobe since the thyroxine content of the homogenates was undetectable. In this respect the elasmobranch is unlike the mammal where the neural lobe does concentrate thyroxine (see review by Pitt-Rivers and Tata, 1959).

Histological methods have previously been used to assay the state of thyroid activity. In order to determine whether such techniques would detect stimulation resulting from incubation of thyroids with whole pituitary homogenates, interferometric measurements on the colloid were made together with a determination of the percentage of the follicular area occupied by epithelium. Neither technique was sensitive enough to detect the stimulation observed by measuring changes in the release of thyroxine (Table 3).

TABLE 1.—Percentage increase in release of thyroxine from *Dasyatis* thyroid tissue produced by adding homogenates of various regions of the *Dasystis* pituitary or lactalbumin hydrolysate to a medium containing salts, urea, and glucose.

Item	*N*	Mean ± SE
Rostral pars distalis (1 lobe/thyroid)	7	43 ± 22
Neurointermediate lobe (1 lobe/thyroid)	8	*31 ± 9
Proximal pars distalis:		
Dorsal lobe (1 lobe/thyroid)	6	40 ± 18
Ventral lobe (1 lobe/thyroid)	7	47 ± 27
Lactalbumin hydrolysate (2 mg/thyroid)	5	35 ± 24

* Significantly differs from zero, $P<0.01$.

TABLE 2.—Percentage increase in the release of thyroxine from *Dasyatis* thyroid tissue produced by adding homogenates of various regions of the *Dasyatis* pituitary to a medium containing salts, urea, glucose plus lactalbumin hydrolysate.

Item	*N*	Mean ± SE
Rostral pars distalis	9	30 ± 19
Neurointermediate lobe	9	*55 ± 20
Proximal pars distalis:		
Dorsal lobe	9	19 ± 15
Ventral lobe	9	**123 ± 40

* Significantly differs from zero, $P<0.05$.
** Significantly differs from zero, $P<0.02$.

TABLE 3.—A comparison of the effectiveness of various techniques for determining the response of *Dasyatis* thyroid glands to 3-day stimulation in vitro by homogenates of whole *Dasyatis* pituitaries (1 pituitary/thyroid).

Item	*N*	Mean percentage of control values ± SE
Increase in release of thyroxine	12	*51 ± 16
Increase in area of follicles occupied by epithelium	7	4.4 ± 5.1
Decrease in interferometric measure of dry wt/unit area of colloid	12	63 ± 38

* Significantly differs from zero, $P<0.01$.

DISCUSSION

The present work confirms the unpublished but frequently quoted work of Ferguson et al. (Dodd et al., 1963) in that there is TSH activity in the elasmobranch pituitary and that the greatest concentration is found in the ventral lobe where gonadotropic activity has also been found (Dodd, Evennett, and Goddard, 1960). The finding of lesser amounts of TSH activity in the neurointermediate lobe is in agreement with the finding of Goddard and Dodd (unpublished but quoted by Dodd et al., 1960). However, their suggestion that the activity is due to a thyrotropin releasing factor cannot explain the present results obtained in vitro with thyroid tissue. The nature of the neurointermediate thyroid stimulating substance is unknown. Dodd et al. (1963) reported that it is heat stable, whereas the activity of the dogfish ventral lobe is not. However, it is not possible to argue that the activity in the neurointermediate lobe is nonprotein since all the activity present in the frog (*Rana temporaria*) pituitary is heat stable and some at least of this is presumed to be the protein TSH.

The comparison of techniques for the demonstration of TSH activity of the pituitary homogenates on the thyroid clearly indicates the inadequacy of histological methods. In spite of a highly significant increase in the release of thyroxine there was no change observed in the follicular epithelium nor in measurements on the colloid weight per unit area. This method is capable of detecting the response of teleost thyroid follicles to a 24-hr incubation with mammalian TSH (Bromage and Sage, 1968).

While the results of incubations of thyroid with pituitary homogenates indicate TSH activity is present in the pituitary, they do not indicate whether it is of functional significance. An obvious followup to these experiments would be the removal of the ventral lobe and the measurement of blood thyroxine levels. However, removal of the ventral lobe in this species has not so far been possible due to the close association of this region with the carotid anastomosis.

Furthermore, the analysis of thyroxine in elasmobranch blood by the present methods is difficult due to unknown factors in the blood which interfere with thyroxine analysis. From this study we conclude that TSH activity is present in the elasmobranch pituitary and that most of this activity is in the ventral lobe. However the functional significance of this activity remains to be determined.

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EFFECT OF DRYING AND DESOLVENTIZING ON THE FUNCTIONAL PROPERTIES OF FISH PROTEIN CONCENTRATE (FPC)

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ABSTRACT

Experiments were performed to determine the effects of drying and steam desolventizing on the functional properties of fish protein concentrate (FPC). The FPC's were produced by a room temperature extraction of either red hake or menhaden with azeotropic isopropyl alcohol. FPC's thus produced contained about 36% soluble protein and, when dried at ambient temperature and pressure, showed very little loss in protein solubility. Drying the extracted wet solids at 40° to 50°, 60° to 70°, 90° to 100°, or 140° to 150°C for 30 or 120 min produced decreased protein solubility, i.e., 30.7% (40° to 50°C) to 12.5% (100° to 120°C). Emulsion stability of an FPC-water-oil system was satisfactory with all samples except those dried at 140° to 150°C.

Desolventizing dry solids or alcohol wet solids by steam stripping produced a dramatic loss in soluble protein and emulsion stability. There was also a significant darkening in color of the FPC's desolventized as wet solids as compared to FPC's desolventized as dry solids.

Food protein additives are used because of their nutritional and/or functional properties. Functional properties include solubility, dispersibility, water holding capacity, and emulsifying capacity (Johnson, 1969, 1970). FPC (fish protein concentrate) can have a range of functional properties depending upon the processing methods used. It is necessary, however, to control certain processing parameters in order to retain functionality.

Extraction of fish with IPA (isopropyl alcohol) at 20° to 30°C produces an FPC with better functional properties than extraction at 50°C (Dubrow, 1971). Similar results have been obtained by extracting chicken protein with IPA (Toledo, 1970).[2] Although low temperature extracted FPC retains a certain degree of protein solubility and emulsifying capacity, these properties may be lost during subsequent drying and desolventizing of the wet solids. Drying and desolventizing is necessary to reduce the residual IPA to 250 ppm to meet FDA (Food and Drug Administration) regulations (Federal Register, 1967). The purpose of the present studies, therefore, was to determine the effect of time and temperature of drying and desolventizing on the functional properties of FPC.

EXPERIMENT I: EFFECT OF TIME AND TEMPERATURE OF DRYING ON FUNCTIONAL PROPERTIES

MATERIALS AND METHODS

Preparation of Samples

Whole red hake (*Urophycis chuss*) were obtained from Block Island off the coast of Pt. Judith, R.I. They were iced on board the fishing vessel and then frozen at dockside. The extraction process consisted of a five-stage cross-current batch extraction at 22° to 27°C. The solvent to raw fish ratio was 2:1 w/w. Each

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extraction stage was limited to 10 to 15 min followed by centrifugation of the solids from liquid. Under these conditions of extraction, the residual lipid in the FPC is reduced to less than 0.5%. Approximately 10 lb. from the last stage centrifuged wet solids were used for drying experiments.

To dry the wet solids, approximately 454 g of wet solids were placed in an aluminum foil dish and spread evenly to a depth of about 6.5 mm. Thermocouples were inserted into the bed of solids for temperature recording. The sample was then placed into a vacuum oven and subjected to drying temperatures of (1) 40° to 50°C, (2) 60° to 70°C, (3) 90° to 100°C, (4) 110° to 120°C, or (5) 140° to 150°C for either 30 or 120 min. Residence time was from the time the sample reached temperature. The sample, after drying, was milled in a Wiley mill[3] and passed through a 40-mesh screen. The samples were then placed into polyethylene bags for storage and subsequent analysis. A control was dried overnight at ambient temperature and pressure.

Methods of Analysis

The following properties were determined:

Salt soluble protein.—Two grams of FPC were added to 50 ml of cold 5% NaCl (in 0.02 M $NaHCO_3$) and magnetically stirred for 3 hr (Dubrow, 1971). The slurry was filtered through Whatman #1 filter paper. The filtrate was analyzed for nitrogen by Kjeldahl method (Horwitz, 1965). Protein was calculated as N × 6.25.

Emulsion stability.—Two grams of FPC were blended (Waring blender, Model #1083) in a pint-size jar with 20 ml of 5% NaCl (in 0.02 M $NaHCO_3$) for 3 min at low speed. Twenty ml of corn oil were added to the blender and the entire mixture blended for 1.5 min at low speed. Ten ml portions of the mix were then poured into three graduated test tubes. The tubes were placed in a water bath (at about 98°C) for 30 min and were then cooled in an ice water bath. Since FPC is more lipophylic than hydrophylic, measurements were taken of the volume of water separated. If oil separated at the same time, measurements were also taken of this phase. Emulsion stability was calculated as the percentage of water (total) that separated from the system.

Residual isopropyl alcohol.—Residual IPA was determined according to the method of Smith and Brown (1969).

Total volatiles.—Total volatiles were determined by placing a weighed sample in a 103°C oven overnight; cooling in a dessicator and reweighing.

RESULTS AND DISCUSSION

Table 1 shows the results of drying temperature and time upon the protein solubility of the FPC solids. The wet solids, prior to drying, had about 36.6% soluble protein. In comparison, wet solids produced by extraction at 70° to 80°C prior to drying contained only 3% soluble protein. Drying overnight under ambient conditions resulted in very little loss in solubility (36.4%). Vacuum drying at 40° to 50°C showed a 15-18% decrease in soluble protein over the ambient dried sample. Variable and unexplainable results were obtained by drying at 60° to 70°C: the soluble nitrogen was less after 30 min drying than after 120 min. Increasing the drying temperature to 90° to 100°C or to 110° to 120°C produced a further decrease in protein solubility. Drying at 140° to 150°C resulted in about a 65% decrease in solubility from the starting wet solids.

The emulsifying stability of the dried FPC's produced under the various conditions of drying, showed that all treatments, except the FPC's dried at 140° to 150°C formed stable oil:water emulsions (Table 1). Separation of oil and water occurred with the FPC's dried at 140° to 150°C.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Effect of drying temperature and time on the salt soluble protein and emulsifying capacity of FPC.

Temperature	Time	Kjeldahl soluble nitrogen[1]	Soluble protein (N × 6.25)		Emulsifying capacity
°C	hr	mg N/ml	% dry wt	$\bar{x}$	% water separated
Wet solids	--	1.17 ± 0.08	36.56	36.56	
Ambient	16.0	2.10 ± 0.04	36.43	36.43	0
40-50	0.5	1.80 ± 0.08	31.33		0
	2.0	1.76 ± 0.08	29.99	30.66	0
60-70	0.5	1.44 ± 0.03	24.06		0
	2.0	1.81 ± 0.11	31.46	27.76	0
90-100	0.5	1.76 ± 0.09	28.92		0
	2.0	1.62 ± 0.10	26.88	27.90	0
110-120	0.5	1.31 ± 0.04	21.64		0
	2.0	1.29 ± 0.03	21.42	21.53	--
140-150	0.5	0.84 ± 0.01	13.55		100
	1.0	0.77 ± 0.01	12.19		100
	2.0	0.73 ± 0.02	11.70	12.48	100

[1] Mean ± standard deviation.

The effects of drying times and temperatures on the residual IPA and total volatiles are shown in Table 2. The sample of FPC dried overnight, under ambient conditions, had a residual IPA content of 2.0%. The samples dried at 40° to 50°C averaged 2.76% IPA; 60° to 70°C averaged 2.62%; 90° to 100°C averaged 2.53%; 110° to 120°C averaged 2.42%; and 140° to 150° averaged 1.45%. Retention of alcohol residues of about 1 to 2% has been obtained even under prolonged drying for up to 4 hr at 70° to 80°C.

TABLE 2.—Effect of drying temperature and time on the total volatile and residual isopropyl alcohol contents of FPC.

Temperature	Time	Total volatiles	Residual isopropyl alcohol[1]	
°C	hr	%	%	
Wet solids		50.00		
Ambient	16	9.94	2.00 ± 0.09	
40-50	0.5	10.25	2.47 ± 0.09	2.76
	2.0	8.30	3.05 ± 0.17	
60-70	0.5	6.50	2.85 ± 0.13	2.62
	2.0	10.10	2.40 ± 0.14	
90-100	0.5	4.90	2.75 ± 0.19	2.53
	2.0	5.85	2.32 ± 0.13	
110-120	0.5	5.40	2.55 ± 0.06	2.42
	2.0	5.90	2.30 ± 0.14	
140-150	0.5	3.20	1.50 ± 0.14	1.45
	2.0	2.45	1.40 ± 0.18	

[1] Mean ± standard deviation and mean of the two groups combined.

In general, the total volatile content of the FPC's ranged from 5 to 10% except those dried at 140° to 150°C, which contained from 2.4 to 3.2% volatiles.

EXPERIMENT II: EFFECT OF DESOLVENTIZING ON FUNCTIONAL PROPERTIES

The results obtained from the drying tests were used to set up the second phase—desolventizing. Thus, the solids dried at ambient temperatures, which yielded the least loss in protein solubility, were used to steam desolventize. Also, the effect of desolventizing wet solids was determined. In this phase, whole menhaden (*Brevoortia tyrannus*) were used for solvent extraction because previous observations had shown this species to be subject to greater color differences than red hake.

MATERIALS AND METHODS

Preparation of Samples

Twenty pounds of whole menhaden were extracted with IPA by the same manner as described for hake in Experiment I. After extraction, one-half of the wet solids were dried at ambient temperature and pressure overnight

and were then steam desolventized. The other half was desolventized as wet solids.

Desolventizing consisted of placing approximately 454 g of either wet solids or dry solids in an autoclave and steaming (exhaust vent open) at 2 to 3 psi for 0, 5, or 10 min. Time of exposure was determined from the time when the autoclave reached pressure, which took about 2 min. After stripping, the sample was dried overnight at ambient conditions and then milled through a 40-mesh screen.

Methods of Analysis

Tests for soluble protein, emulsion stability, residual IPA, and total volatiles were as reported in the experiments on drying. Color of the samples was determined by reflectance analysis (Dubrow, 1971), using a Beckman DB Spectrophotometer with reflectance attachment. Reflectograms were obtained by scanning from 700 mμ to 390 mμ.. Analysis of color was also determined on a Hunter Color Meter, Model D25.

RESULTS AND DISCUSSION

Desolventizing Wet Solids

Table 3 shows the effect of steam desolventizing wet solids on the salt soluble proteins, emulsion stability, color, residual IPA, and total volatiles.

The protein solubility of FPC's decreased from 32.3% in the nonsteamed solids to between 8.6 and 10.5% in the steamed solids. The loss in solubility occurred during the come-up period as evidenced by the low soluble protein content of the solids from the 0 min treatment.

The loss in protein solubility was also accompanied by a loss in emulsion stability. All treatments resulted in a separation of phases; emulsion, water, and solids. About 20 to 25% of the water separated from the mixture.

The effect of steaming to remove IPA showed that after 5 min the residual alcohol was less than 250 ppm, decreasing from 30,000 ppm at 0 min to 200 ppm after 5 min and to 75.5 ppm after 10 min. The total volatiles of the FPC's were 7.8%, 5.3%, and 4.9%, respectively.

Steam desolventization of wet solids changed the color of the FPC's. A significant darkening, from a grayish tan to a grayish brown, occurred in those samples steamed for 5 and 10 min. A reflectance spectra of the 0-min and 10-min treatments is shown in Figure 1. Hunter L, a, and b values are presented in Table 3.

Desolventizing Dry Solids

Table 3 also shows the effects of steam desolventizing dry solids on protein solubility, emulsion stability, color, residual IPA, and total volatiles. The initial protein solubility, prior to treatment, was 28.2%. Although steaming the FPC for 0 min did not result in any great loss in protein solubility, the 5-min and 10-min steamed samples showed about a 57% loss in

TABLE 3.—Effect of steam desolventizing FPC wet solids and FPC dry solids on the salt soluble protein, emulsifying capacity, color, and volatile content.

Sample	Time	Salt soluble protein	Emulsifying capacity	Color			Residual isopropyl alcohol	Total volatiles
				L	a	b		
	min	*% of dry wt*	*% water separated*				*ppm*	*%*
Wet solids:								
Nondesolventized	--	32.29	--	--	--	--	--	--
	0	9.49	[1]20.0	62.02	+0.30	+11.72	30,000	7.76
	5	8.57	[1]24.3	52.94	+0.35	+11.76	200	5.29
	10	10.52	[1]20.7	50.83	+0.71	+11.22	75.5	4.91
Dry solids:								
Nondesolventized	--	28.23	0.0	--	--	--	55,000	11.44
	0	26.70	0.0	65.65	−0.60	+10.75	24,500	6.38
	5	12.71	[1] 5.0	62.12	−0.07	+12.15	1,000	5.35
	10	10.68	[1]15.0	61.71	−0.08	+12.50	367	4.91

[1] Separation into three phases: water, solids, emulsion.

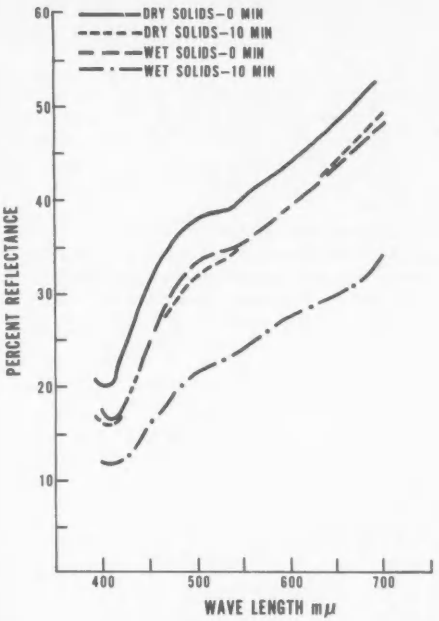

FIGURE 1.—Reflectance spectra of FPC's steam desolventized, as either dry solids or alcohol wet solids, at 2 to 3 psi for 0 or 10 min.

protein solubility as compared to the nonsteamed sample.

The emulsifying capacity and stability of the treated solids was affected in a manner similar to that for protein solubility. Both the nonsteamed and the 0-min treated samples of FPC's emulsified in oil and water systems. On the other hand, the solids steamed for 5 and 10 min showed a decrease in emulsion stability.

Steam desolventization of the dry solids reduced the residual IPA with each increment of exposure time. The initial residual content was 55,000 ppm, and after 10 min the level was found to be 367 ppm. The total volatiles of the treated solids ranged from 6.4% (0 min) to 4.9% (10 min).

The color of the FPC's after steaming showed only a slight darkening. The color changed from a grayish tan to a slight yellowish tan with respect to time of exposure. Hunter L, a, and b values are presented in Table 3. Figure 1 illustrates the reflectance spectra for the 0-min and 10-min FPC's and shows that the 10-min steamed dry solid sample was similar in its reflectance to the 0-min steamed wet solid sample; whereas the 0-min steamed dry solid was much lighter.

CONCLUSIONS

Two critical steps in the preparation of FPC by low temperature extraction with IPA are the drying and the desolventizing. Both stages involve heating: either dry or moist heat, or both. The results of this study showed that drying alcohol wet FPC solids at ambient conditions resulted in negligible loss in soluble protein and emulsifying capacity. Hot air drying of the wet solids, under vacuum, at temperatures ranging from 40° to 50°C to 110° to 120°C for 30 or 120 min resulted in a temperature dependent decrease in protein solubility. The dry FPC's, however, still retained emulsifying capacity. Under these drying conditions, the residual IPA was reduced to 2 to 3%. Higher drying temperatures of 140° to 150°C resulted in further loss of protein solubility and a complete loss in emulsifying capacity.

Removal of residual IPA, to a level of less than 250 ppm, by steam desolventization, was faster for wet solids than for dry solids. This procedure, however, brought about a 70% loss in protein solubility, a complete loss in emulsion stability, and a significant darkening of the product as compared to steam dry solids.

A similar loss in functionality, but at a slower rate and with less darkening of the FPC's, resulted from steaming dry solids.

Low temperature extraction coupled with low temperature drying produced FPC with greater functional properties than that produced by high temperature drying. To retain this functionality, methods other than steaming appear to be necessary.

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FISH LARVAE OF THE ESTUARIES AND COAST OF CENTRAL MAINE

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ABSTRACT

Seasonal sampling of fish larvae in the central Maine coast took 22 kinds of larvae; 17 were identified to species, 3 to family, and 2 were not identified. Larvae of a few highly abundant species were present in the winter and early spring. These hatched from demersal eggs and were concentrated in the upper estuaries. The remaining species were less abundant and were present during the spring and summer. Most of these larvae hatched from pelagic eggs and were not greatly concentrated in the upper estuaries. The larvae of only one commercially important species, *Clupea harengus harengus*, were found abundantly in the region.

There is little information on the species composition and abundance of larval fishes in the numerous estuaries and bays of the coast of Maine. During the past 10 years (1961-70) samples of larval herring have been taken in the central area of the Maine coast for a program of research on the prerecruit stage of the herring. In three of those years (1961, 1968, and 1970) other fish larvae also were identified. An examination of the first year's catch was reported by Graham and Boyar (1965). This paper reports on the 1968 and 1970 identifications and gives a more complete picture of the seasonal abundance and spatial distribution of the larvae; it also compares the results with surveys in other adjacent areas.

The area sampled is a system of drowned river valleys and bays typical of the Maine coast. It is bounded on the west by the Sheepscot estuary and on the east by the Damariscotta estuary, extends offshore approximately 4 miles to lat 43°45'N, and will be referred to in this report as the Boothbay region. The general ecology of the Sheepscot estuary was described by Stickney (1959), and the hydrography of the area was reported by Graham and Boyar (1965). The portion of the Sheepscot estuary sampled during this study is 14 miles long, has a drainage area of 148 square miles, varies from 20 to 60 m in depth, and is more typical of a long, narrow bay than an estuary. The portion of the Damariscotta estuary sampled is 11 miles long, has more freshwater dilution in its upper portion than the Sheepscot, and has a smaller drainage basin. The bay separating the two estuaries is a typical coastal indentation with relatively deep water, steep rocky shores, and very little freshwater dilution.

Other surveys of fish eggs and larvae from areas close to the coastal Gulf of Maine are pertinent to this study. Perlmutter (1939) and Wheatland (1956) identified the larvae from Long Island Sound, and Merriman and Sclar (1952) from Block Island Sound. Herman (1963) reported on the fish eggs and larvae of Narragansett Bay, R.I., and Pearcy and Richards (1962) on those of the Mystic River estuary, Conn. Marak and Colton (1961), Marak, Colton, and Foster (1962), and Marak, Colton, Foster, and Miller (1962) have reported for the offshore area of Georges Bank and the Gulf of Maine, and Fish and Johnson (1937) for the Gulf of Maine and Bay of Fundy.

METHODS

Eight stations were sampled twice a month from January through August 1968 and from November 1969 through October 1970 (Figure 1). Additional information was available from occasional sampling in 1971. The larvae were

[1] Northeast Fisheries Center, National Marine Fisheries Service, NOAA, West Boothbay Harbor, ME 04575.

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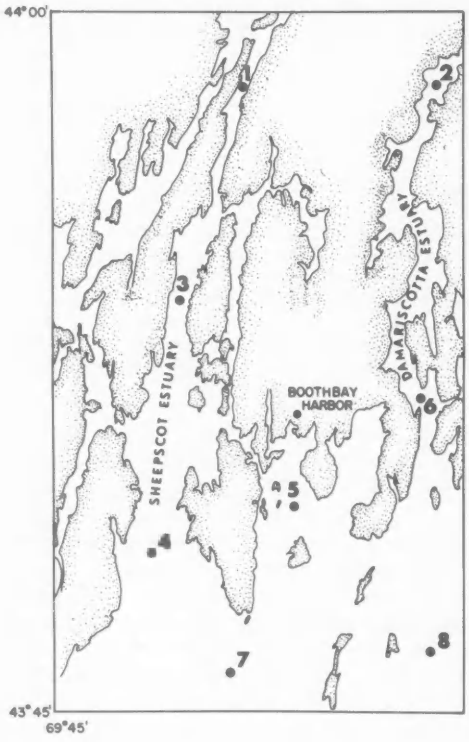

FIGURE 1.—Sampling stations in the Boothbay region, January through August 1968 and November 1969 through October 1970.

preserved in 5% Formalin[2] and identified in the laboratory. The stations were grouped according to general location within the sampling area and are termed upper estuarine stations (1, 2, and 3), lower estuarine stations (4, 5, and 6), and outer stations (7 and 8). The outer stations were approximately 4 miles from the headlands.

Larvae were collected with a Boothbay Depressor Trawl (Graham and Vaughan, 1966) using a 3-stepped oblique tow (10 min each level) from bottom to surface. The trawl was towed at 4 knots for 30 min. The amount of water strained was determined by using the opening of the net and the distance towed. The mesh opening of the trawl net (2 mm) was larger than that of the meter net (0.51 mm) used by Graham and Boyar (1965). Small larvae (<2 mm) probably escaped through the larger mesh, but the species composition of the larvae caught in both the Boothbay Depressor Trawl and meter net was similar.

Larval identification was based on known spawning time and on previously reported identifications. References used most often in identification were Colton and Marak (1969), Bigelow and Schroeder (1953), and Graham and Boyar (1965).

RESULTS

Twenty-two kinds of larvae were represented in the collections in the Boothbay region during January to August 1968 and November 1969 to October 1970 (Table 1); 17 kinds were identified to species, 3 to family, and 2 were not identified. All of the species were boreal with centers of abundance north of the mid-Atlantic coast, and many of the more abundant larvae do not occur south of New England. Most of the larvae, particularly the more abundant ones, hatch from demersal eggs.

SPECIES ABUNDANCE AND COMPOSITION

Larvae were most abundant during late winter to early spring (Figure 2). The dominant larvae at this time were *Pholis gunnellus*, *Liparis* sp., *Cryptacanthodes maculatus*, *Lumpenus lumpretaeformis*, and the Cottidae; they represented 91% of the total catch. In addition, *Anguilla rostrata* and a species of Gadidae (probably *Gadus morhua*) occurred in small numbers (0.1% and 0.01% of the total catch). The composition of the dominant kinds of larvae differed between years. The Cottidae was dominant in 1968 and *P. gunnellus* in 1970; *C. maculatus*, *L. lumpretaeformis*, and the *Liparis* sp. were more numerous in 1968 than in 1970.

Catches of larvae in the winter and early spring were large between February and April

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Larval fish taken in the central Maine coast region January to August 1968 and November 1969 to October 1970.

Scientific name	Common name	Number of larvae		Egg deposition
		Jan.-Aug.	Nov.-Oct.	
Cottidae	Sculpins	6,222	4,053	Demersal
Pholis gunnellus (Linnaeus)	Rock gunnel	2,336	5,531	Demersal
Liparis sp.	Seasnail	1,610	106	Demersal
Anguilla rostrata (Lesueur)	American eel	19	11	Unknown
Cryptacanthodes maculatus Storer	Wrymouth	164	96	Unknown
Lumpenus lumpretaeformis (Walbaum)	Snakeblenny	328	225	Demersal
Gadidae	Codfishes	3	0	Pelagic
Aspidophoroides monopterygius (Bloch)	Alligatorfish	139	29	Unknown
Merluccius bilinearis (Mitchill)	Silver hake	0	4	Pelagic
Ammodytes americanus DeKay	American sand lance	0	2	Demersal
Sebastes marinus (Linnaeus)	Redfish	4	1	Ovoviviparous
Cyclopterus lumpus Linnaeus	Lumpfish	4	5	Demersal
Limanda ferruginea (Storer)	Yellowtail flounder	22	17	Pelagic
Osmerus mordax (Mitchill)	Rainbow smelt	12	0	Demersal
Syngnathus fuscus (Storer)	Northern pipefish	15	2	Oviparous
Scophthalmus aquosus (Mitchill)	Windowpane	23	8	Pelagic
Ulvaria subbifurcata (Storer)	Radiated shanny	127	82	Unknown
Enchelyopus cimbrius (Linnaeus)	Fourbeard rockling	21	3	Pelagic
Clupea harengus harengus Linnaeus	Atlantic herring	619	792	Demersal
Tautogolabrus adspersus (Walbaum)	Cunner	8	11	Pelagic
Species A		0	5	Unknown
Species B		117	22	Unknown

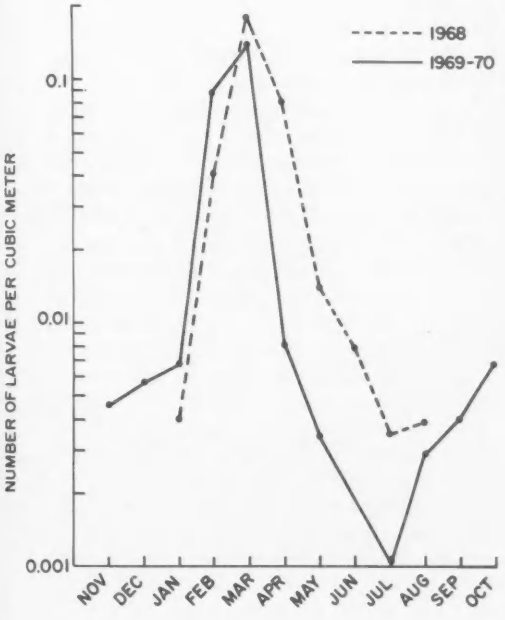

FIGURE 2.—Seasonal abundance of fish larvae in the Boothbay region, January through August 1968 and November 1969 through October 1970.

and largest during the first half of March. In both years the catches were similar. The average for the March peak was 0.18 per m^3 in 1968 and 0.14 per m^3 in 1970 and for the period between February and April, 0.08 per m^3 in 1968 and 0.09 per m^3 in 1970. The larvae were abundant longer in 1968 than in 1970; the large catches in 1968 extended into April and May.

In spring the numbers of larvae in the catch declined sharply with the end of the larval stage of the dominant species and continued gradually to decline to a low point in July and August. Most of the remaining larvae were taken in the spring and summer and, although fewer in numbers, more species were present. Species in this group were: *Aspidophoroides monopterygius, Merluccius bilinearis, Ammodytes americanus, Sebastes marinus, Cyclopterus lumpus, Limanda ferruginea, Osmerus mordax, Syngnathus fuscus, Scophthalmus aquosus, Ulvaria subbifurcata, Enchelyopus cimbrius, Tautogolabrus adspersus.* Of these, *U. subbifurcata* and *E. cimbrius* were obtained as larvae into the fall. *Clupea harengus harengus* hatched in September and October and was present in the area as larvae through May. The increased larval abundance in September and October was due to the hatching

of *Clupea harengus harengus* which was the only species abundant in the autumn.

The distribution of the larvae from offshore to the upper estuaries changed seasonally. Catches from the upper estuarine, lower estuarine, and outer stations (Figure 3) showed that the larvae in the winter and early spring were concentrated in the upper estuaries, while the larvae in the summer were more evenly distributed.

The upper estuaries are probably important as nursery areas for the winter-early spring larvae. Most of this group were captured within the estuaries. From January to May the three upper stations contributed 68% of the catch in 1968 and 70% of the catch in 1970. Station 2 in the upper Damariscotta estuary produced the highest catches, accounting for 40% of all the larvae taken in 1968 and 65% in 1970. The distribution of the winter-early spring group of larvae was different within the estuaries between years. In 1968 the larvae were more evenly distributed among the upper stations than in 1970.

The seasonal abundance for each kind of larvae taken in the Boothbay region is shown in Figures 4 and 5. The more common kinds are discussed below.

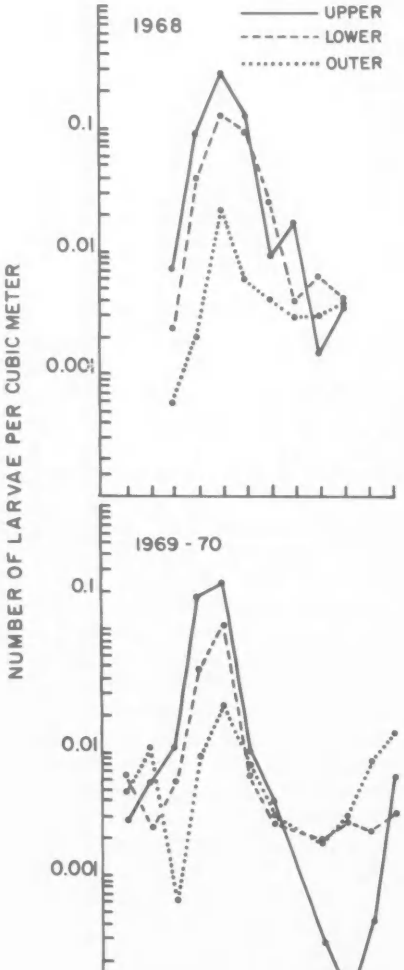

FIGURE 3.—The seasonal abundance of fish larvae in three areas of the Boothbay region; the upper estuary, the lower estuary, and outside the headlands.

Cottidae

Cottid larvae were present from January to July and their abundance reached a peak in March. Their distribution was upper estuarine and they were most abundant at station 2 (50% of all cottids in 1968, 74% in 1970). The total abundance of these larvae differed between years (6,222 in 1968 and 4,053 in 1970) because more cottids were taken at the other stations in 1968 (Figure 4A). Spawning probably occurred in the upper estuaries, inasmuch as cottids lay demersal eggs which do not drift, and yolk sac larvae were taken at the upper stations.

All cottid larvae were not identified to species, but Nuzrat Khan, Department of Biology, University of Ottawa, Ottawa, Canada (personal communication) recognized five species from 1,387 specimens of cottids that I sent to him. Of these, 689 were *Myoxocephalus scorpius;* 456, *Myoxocephalus octodecemspinosus;* 183, *Myoxocephalus aenaeus;* and 59, *Triglops* sp.

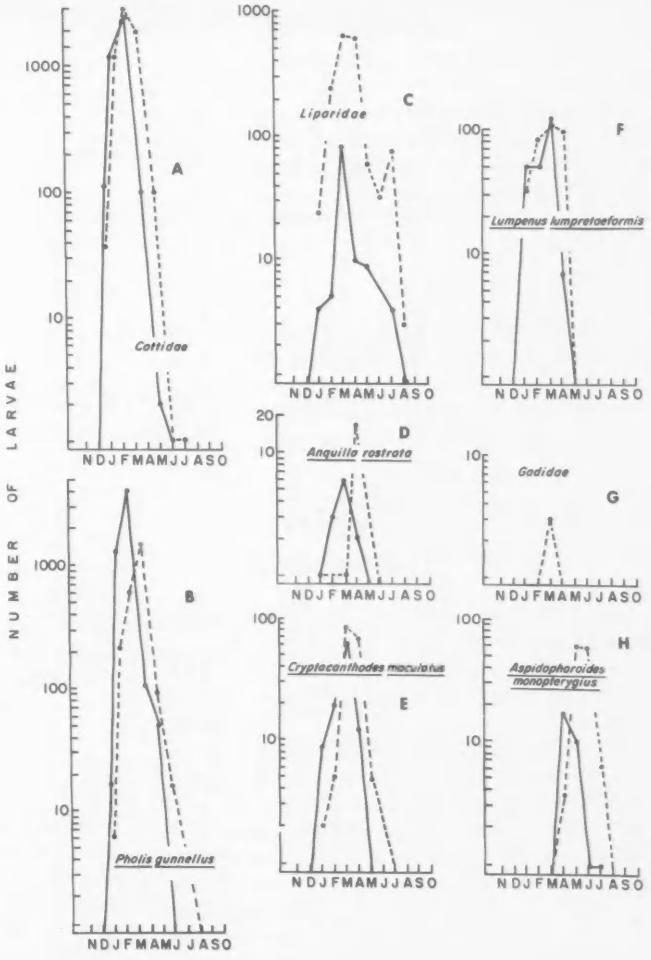

FIGURE 4.—Seasonal abundance of the following kinds of fish larvae in the Boothbay region, January through August 1968 and November 1969 through October 1970: A. Cottidae, B. *Pholis gunnellus*, C. Liparidae, D. *Anguilla rostrata*, E. *Cryptacanthodes maculatus*, F. *Lumpenus lumpretaeformis*, G. Gadidae, H. *Aspidophoroides monopterygius*.

Pholis gunnellus

The eggs of *P. gunnellus* are demersal, and yolk sac larvae were found in the upper estuaries during this study, suggesting that they were spawned there. The larvae appeared in the catches from January to July and reached peak abundance in February and March (Figure 4B). They represented 20% of the catch in 1968 and 50% of the catches in 1970. Their distribution was upper estuarine and, like cottids, they were most abundant at station 2 (28% of the catch in 1968 and 59% in 1970).

Liparis sp.

Liparid larvae were common in our catches in 1968 (14% of the catch) but less so in 1970 (1%) (Figure 4C). They probably spawn within the estuaries as they lay demersal eggs, and yolk sac larvae were found in the upper estuaries. The greatest number were taken in

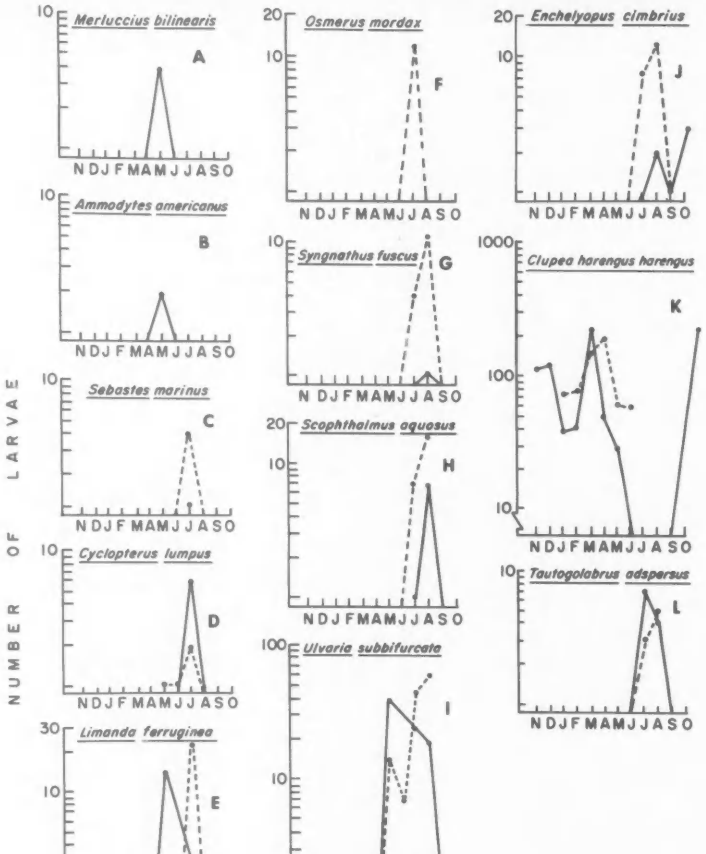

FIGURE 5.—Seasonal abundance of the following kinds of fish larvae in the Boothbay region, January through August 1968 and November 1969 through October 1970: A. *Merluccius bilinearis*, B. *Ammodytes americanus*, C. *Sebastes marinus*, D. *Cyclopterus lumpus*, E. *Limanda ferruginea*, F. *Osmerus mordax*, G. *Syngnathus fuscus*, H. *Scophthalmus aquosus*, I. *Ulvaria subbifurcata*, J. *Enchelyopus cimbrius*, K. *Clupea harengus harengus*, L. *Tautogolabrus adspersus*.

the upper estuaries, and the difference in abundance between years suggests that there was considerably less spawning in 1970 than 1968.

Lumpenus lumpretaeformis

L. lumpretaeformis probably spawns in the upper estuaries because yolk sac larvae were

found there and egg deposition, although not known, is probably demersal (it is for closely related forms). They were captured from January to April with a peak abundance in March (Figure 4F).

Aspidophoroides monopterygius

A. monopterygius larvae were abundant a little later than the winter-early spring group, ranging from April to July with a peak in April or May (Figure 4H). Their distribution was more lower estuarine than upper.

Ammodytes americanus and *Cyclopterus lumpus*

The larvae of *A. americanus* (Figure 5B) and *C. lumpus* (Figure 5D) were only rarely taken in this study but Graham and Boyar (1965) reported them abundant. However, these authors reexamined some of their specimens identified as *Cyclopterus lumpus* and *Ammodytes americanus* and found that most identified as *C. lumpus* were *Liparis* sp. and many identified as *A. americanus* were *Pholis gunnellus*.

Gadidae

Several kinds of gadids spawn in our sampling area. *Enchelyopus cimbrius* (Figure 5J) was one of the two dominant species from June until October in the lower estuaries and outer areas. A few larvae of *Merluccius bilinearis* (Figure 5A) were taken in May 1970. Three specimens of what was probably *Gadus morhua* (Figure 4G) were taken in March 1968. Subsequent sampling (1971) took a few more *G. morhua* in December as yolk sac larvae and also later stage larvae in February in the Sheepscot estuary.

Ulvaris subbifurcata

This was the other dominant species in the spring and summer (Figure 5I). It was present from April until September in the lower estuaries and outer areas.

Clupea harengus harengus

This is a pelagic species that lays demersal eggs and uses both the estuaries and bays as nursery areas during its larval stage from October to May (Figure 5K). It was the only commercially important species to do so and I would consider these areas important to the population density of the species.

Species A and B

At present we are attempting to identify these species. Species A is probably one of the Stichaeidae, possibly *Lumpenus maculatus*. Species B has been tentatively identified as *Hemitripterus americanus* but needs confirmation.

DISCUSSION

LARVAL NURSERY AREAS

Most of the fishes whose larvae were present in the Boothbay region may be placed in one of two groups: those that use the estuaries as primary spawning and nursery areas and those that do not.

The larvae found in the region during the winter and early spring (*Pholis gunnellus*, *Liparis* sp., *Cryptacanthodes maculatus* (Figure 4E), *Lumpenus lumpretaeformis*, and the Cottidae) belong to the first group. They were the most abundant species and their greatest concentration was in the upper estuaries. They are larvae of resident demersal fish that are not commercially important but are extremely abundant in the area. They use the bays and estuaries as nursery areas, depending to a large extent on these areas for their reproductive success. These species lay demersal eggs in the estuaries. Pearcy and Richards (1962) discussed the possibility that the larvae of demersal species in the Mystic River estuary maintained themselves there by concentrating in the counter currents near the bottom. The stepped oblique tow that was used in my study was not suitable for an analysis of the depth distribution of the larvae. The winter-early spring group of larvae,

however, were most abundant in the upper estuaries throughout their larval life, and therefore probably maintained themselves there by adapting to the circulation of water within the estuaries. These larvae disappeared from the catches very rapidly during April and May, which contributed to the rapidly declining spring catch. By this time they were approaching the juvenile stage and, being benthic fish, probably settled to the bottom and were not available to the sampling gear.

The remaining species (*Merluccius bilinearis, Sebastes marinus* (Figure 5C), *Cyclopterus lumpus, Limanda ferruginea* (Figure 5E), *Syngnathus fuscus, Scopthalmus aquosus* (Figure 5H), *Ulvaria subbifurcata, Enchelyopus cimbrius,* and *Tautogolabrus adspersus* (Figure 5L)) were present but not abundant in the spring and summer, suggesting that the estuaries were not their primary nursery areas. Possibly the numbers of spawning adults of these species were low in the bays and estuaries, or, as most of these species lay pelagic eggs, the eggs were dispersed before the larvae hatched.

Some species did not belong to either of the two above-mentioned groups: *Anguilla rostrata* (Figure 4D), a catadromous, and *Osmerus mordax* (Figure 5F), an anadromous species; *Aspidophoroides monopterygius,* which spawns later than the winter-early spring group, was not as common in the upper estuaries; *Ammodytes americanus*; and the Gadidae.

COMPARISON WITH OTHER AREAS OF THE NORTHWEST ATLANTIC

The results of surveys in other areas of the northwest Atlantic indicate the overall distribution of the three more abundant larvae of the Boothbay region. Cottid larvae occurred throughout the surveyed areas. *Myoxocephalus aenaeus* was dominant in the Mystic River estuary (Pearcy and Richards, 1962), Block Island Sound (Merriman and Sclar, 1952), and Long Island Sound (Wheatland, 1956); *M. octodecemspinosus* occurred in the offshore areas (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962); and *M. scorpius* occurred in the Gulf of Maine (Fish and Johnson, 1937) and appears from my survey to be dominant along the central Maine coast. The larvae of *Pholis gunnellus* appear to be more abundant in the estuaries than offshore. They were one of the most abundant species in the Mystic estuary (Pearcy and Richards, 1961) where they also concentrated in the upper estuaries. They were less abundant in the more open Narragansett Bay (Herman, 1963), rare offshore (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962), and absent from Long Island (Wheatland, 1956) or Block Island Sounds (Merriman and Sclar, 1952). Larvae of the Liparidae were taken in small numbers offshore (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962) and in the Gulf of Maine (Fish and Johnson, 1937) but not at all south of Cape Cod.

Pearcy and Richards (1962) found a dominant winter-early spring group of larvae in the Mystic estuary, but the more abundant species differed from those in the central Maine coast. The dominant species in the Mystic estuary were *Pseudopleuronectes americanus, Microgadus tomcod,* and *Myoxocephalus aenaeus.* In Narragansett Bay (Herman, 1963) the demersal winter-early spring group of larvae was less evident with only *Myoxocephalus* sp. dominant, and with many more pelagic forms. An abundance of pelagic forms might be expected in Narragansett Bay because the Bay is characteristically more like the open ocean than the smaller estuaries.

The spring and summer species of larvae were abundant enough in southern New England (Pearcy and Richards, 1962; Herman, 1963) to create a second summer peak in larval abundance that was absent in my survey of the Boothbay region. This was probably due to the absence of larvae of such species as *Stenotomus chrysops, Anchoa mitchilli, Cynoscion regalis,* and *Tautoga onitis* which have a more southern distribution and are only occasionally taken as adults along the Maine coast (Bigelow and Schroeder, 1953).

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EFFECTS OF TEMPERATURE AND SALINITY ON LARVAL DEVELOPMENT OF GRASS SHRIMP, *PALAEMONETES VULGARIS* (DECAPODA, CARIDEA)[1,2]

PAUL A. SANDIFER[3]

ABSTRACT

Larvae of *Palaemonetes vulgaris* were reared in the laboratory in a factorial experiment employing three temperatures (20°, 25°, and 30°C) and six salinities (5, 10, 15, 20, 25, and 30‰). Temperature and salinity exerted significant effects at the 1% level on survival of larvae through metamorphosis. The temperature-salinity interaction was also significant, but at the 5% level. Lowest survival occurred in 5‰ at all temperatures. In higher salinities, survival at 20° and 25°C was similar (>60%) but was significantly less at 30°C in most salinities. Temperature and salinity also influenced the rate of larval development. Development at 20°C required nearly twice the time as that at 25° and 30°C, but a retarding influence of salinity was slight and evident only at low salinities (5 and 10‰). Considerable variation in the number of larval instars was observed among animals which survived to the postlarval stage. Metamorphosis occurred as early as the fifth molt and as late as the twelfth. Salinity and temperature-salinity interaction had no detectable influence on the number of instars, but the effect of temperature was significant at the 1% level. Larvae reared at 25°C passed through fewer molts prior to metamorphosis than did those reared at 20° and 30°C. Comparing survival, rate of development and number of instars, optimal conditions for larval development occurred at a moderate temperature of about 25°C over a wide range of salinity (10 to 30‰).

The grass shrimp, *Palaemonetes vulgaris* (Say), ranges at least from Barnstable County, Mass., to Cameron County, Tex., (Williams, 1965) and is one of the most abundant estuarine decapods in this range. In the laboratory, Nagabhushanam (1961) found the species to be nearly euryhaline, tolerating salinities from 3 to 35‰. More recently, Bowler and Seidenberg (1971) found *P. vulgaris* to be less tolerant of low salinities (≤3‰) but more tolerant of high salinities (36 and 40‰) than its congener, *P. pugio*. In the York River, Va., these authors found that the percentage of the *Palaemonetes* population made up by *P. vulgaris* decreased markedly with decreasing salinity, and in North Carolina, Knowlton and Williams (1970) found *P. vulgaris* only in waters of 15 to 35‰ salinity.

Only Knowlton (1965, 1970) has studied the effects of temperature and salinity on *P. vulgaris* larvae, and his results were limited by the small number of experimental animals he used. The objectives of the present study were to determine the effects of temperature and salinity on survival and development of *P. vulgaris* larvae reared through metamorphosis in the laboratory.

MATERIALS AND METHODS

The experimental design was a 3 × 6 factorial using temperatures of 20°, 25°, and 30°C and salinities of 5, 10, 15, 20, 25, and 30‰. Test media were prepared by diluting seawater with

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distilled water, and temperature control baths were modified from Reed (1969). Each bath was equipped with a thermostat, two 125-w heaters, a maximum-minimum thermometer, and an air stone to circulate the water. A grate suspended in each bath supported the culture vessels. The baths were placed inside a cold room maintained at 11°C, where a 60-w bulb controlled by a timer provided 14 hr of light every 24 hr, approximately coincident with times of natural daylight. Although the temperature regimes are referred to above and throughout the paper as 20°, 25°, and 30°C, the observed temperatures (mean ± one standard deviation) were 20.3°C ± 0.7°C (range, 18.3° to 21.1°C), 25.4°C ± 1.0°C (range, 22.8° to 26.7°C), and 30.6°C ± 0.5°C (range, 29.4° to 31.7°C), respectively.

An ovigerous female was collected near Wachapreague, Va., on 12 June 1970. Salinity at the collection site was approximately 30‰. The shrimp was maintained in a glass bowl at 30‰ salinity and 25°C in the laboratory, and larvae were obtained on the day following collection. Active larvae were first placed in mass cultures at room temperature and fed newly hatched *Artemia* nauplii (California Brine Shrimp, Inc., Menlo Park, Calif.). Zoeae to be reared in 5, 10, and 15‰ salinity were acclimated in 15‰ for 4 hr, and those to be reared in higher salinities were maintained in 30‰ for 4 hr. Larvae were then transferred with a large-bore medicine dropper to test media in compartmented plastic boxes. Each box contained 18 compartments in rows of six, and one zoea in 50 ml of media was placed in every compartment. Three salinities were tested per box (i.e., each row of six compartments was a replicate of a particular temperature-salinity combination), and there were six boxes in each of the three water baths. Thus, there were three replicates (one in each of three boxes) of each temperature-salinity combination, and a total of 18 larvae was reared at each condition.

Larvae were transferred to clean boxes with fresh media and fed an abundance of newly hatched *Artemia* nauplii once daily. Molts, deaths, and maximum and minimum temperatures were recorded at this time. Mean temperatures and standard deviations were calculated from the maximum and minimum temperatures. The experiment was terminated after 40 days, when all survivors were in postlarval stages.

RESULTS

A detailed presentation of survival and developmental history of each larva reared in the present study is given in Appendix Table 1.

SURVIVAL

In general, survival was similar (>60%) at 20° and 25°C but was lower at 30°C in nearly all salinities. Survival in 5‰ salinity occurred only at 25°C, where 13 zoeae successfully completed the first molt, and two survived through metamorphosis; in contrast, at 20° and 30°C only two zoeae molted once, and none survived to molt again.

An analysis of variance on arcsin transformations (Steel and Torrie, 1960) of the percentage survival data showed differences in survival between temperatures and between salinities at the 1% level, and the temperature-salinity interaction was significant at the 5% level (Table 1). Student-Newman-Keuls' multiple range tests (Steel and Torrie, 1960) were used to explain the significant differences (Table 2). Perhaps the simplest way of looking at these differences in Table 2 is to compare survival in each salinity under each of the different temperatures, as is shown graphically in Figure 1. Thus, between 20° and 25°C there were significant differences in survival only in 5 and 30‰ salinity. Survival at 25°C, 5‰ was significantly greater than that at 20°C, 5‰, while at 20°C, 30‰ survival was significantly greater than at 25°C, 30‰. Comparing 20° and 30°C, survival at 20°C was significantly greater than that at 30°C in 10, 15, and 25‰. Finally, comparing 25° and 30°C, survival at 25°C was significantly greater than that at 30°C in 5, 10, 15, and 25‰. Highest overall percentage survival (88.9%) occurred at the combination 20°C, 20‰ (Table 2, Figure 1).

TABLE 1.—Analysis of variance for differences in survival of *Palaemonetes vulgaris* larvae through metamorphosis under different conditions of temperature and salinity.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*
Temperature	2	4,912.0345	2,456.0172	17.8613**
Salinity	5	21,212.5667	4,242.5133	30.8535**
Temperature × salinity	10	3,842.1588	384.2158	2.7941*
Error	36	4,950.1734	137.5048	
Total	53	34,916.9334		

** Significant at 1% level.
* Significant at 5% level.

TABLE 2.—Summary of Student-Newman-Keuls' multiple range tests to explain differences in survival of *Palaemonetes vulgaris* larvae at different temperature and salinity conditions.

Experimental conditions		Mean (transformed % survival)	Means not overlapped by the same line are significantly different at the 1% level
°C	‰		
30	5	0.0	
20	5	0.0	
25	5	16.1	
30	10	24.1	
30	15	31.5	
30	25	38.5	
25	30	52.0	
30	20	58.5	
30	30	58.5	
20	25	58.5	
25	10	62.2	
25	20	62.2	
20	30	65.9	
20	10	66.5	
25	25	67.0	
25	15	70.2	
20	15	70.2	
20	20	73.9	

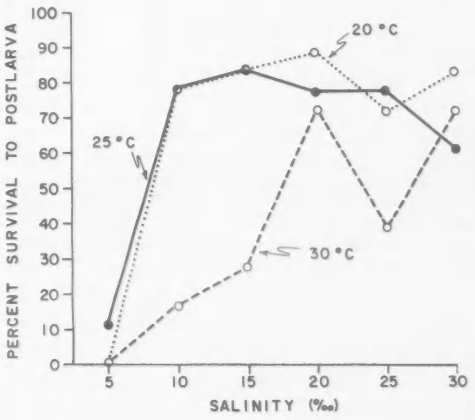

FIGURE 1.—Comparison of survival to postlarvae for *Palaemonetes vulgaris* zoeae reared at different temperatures and salinities.

RATE OF DEVELOPMENT

The effects of temperature and salinity (excluding 5‰) on the rate of larval development are shown in Figure 2. The effect of temperature was pronounced; development at 20°C was much slower than at 25° or 30°C. Mean duration of development (days) ± one standard deviation was 30.2 ± 3.8 (range, 23 to 39) at 20°C, 16.6 ± 2.7 (range, 14 to 25) at 25°C, and 15.7 ± 1.8 (range, 13 to 21) at 30°C. Salinity influenced the rate of development much less than did temperature. Survival in 5‰ salinity occurred only at 25°C, where the larvae in 5‰ generally required about 1 to 4 more days to pass a given stage than did larvae in higher salinities at the same temperature. Development in 10‰ also tended to be slightly slower than in higher salinities, regardless of the temperature (Figure 2). There was little apparent difference among developmental rates in 15 to 30‰. In general, a Q_{10} (20° and 30°C) of about 1.8 was typical of larval development.

Mean duration of instars (Table 3) was inversely related to temperature, reflecting developmental rate. Duration of successive instars tended to increase slightly at 20°C. The second instar was markedly short at 25° and 30°C, and the final instar was of longest duration at all temperatures. Overall mean instar duration (days) ± one standard deviation for animals which completed development was 3.6 ± 0.8 (range, 3 to 7) at 20°C, 2.2 ± 0.7 (range, 1 to 7) at 25°C, and 1.9 ± 0.6 (range, 1 to 4) at 30°C.

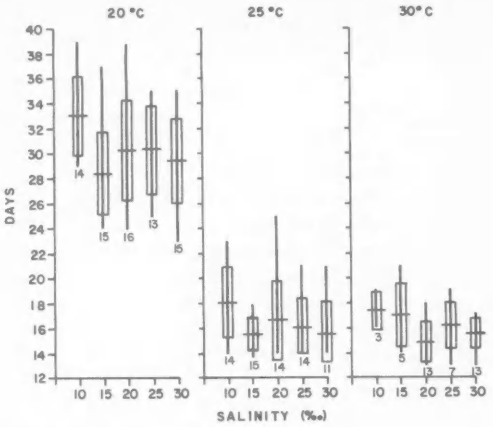

FIGURE 2.—Mean ± one standard deviation and range of days required for *Palaemonetes vulgaris* larvae to reach the postlarval stage at different temperatures and salinities (5‰ excluded) (numbers at the lower end of each range line indicate the number of animals which reached the postlarval stage at those conditions of temperature and salinity).

TABLE 3.—Mean duration (days) of *Palaemonetes vulgaris* larval instars at different temperatures. Final instar treated separately.

Instar	Temperature (°C)		
	20	25	30
	Days	*Days*	*Days*
I	3.0	2.0	2.0
II	3.1	1.4	1.0
III	3.1	2.0	1.2
IV	3.2	2.0	1.9
V	3.5	2.1	1.9
VI	3.8	2.1	2.0
VII	3.9	2.1	2.0
VIII	3.5	2.4	2.0
IX	3.7	[1]2.2	[1]1.8
X	[1]4	[1]2	--
XI	--	[1]2	--
Final	5.0	3.3	2.9

[1] Based on five or fewer larvae.

VARIATION IN NUMBER OF INSTARS

Most larvae metamorphosed at the 7th, 8th, or 9th molt, but there was much variation in number of instars. Metamorphosis occurred at the 5th through the 12th molts, and one zoea passed through 12 zoeal instars but never reached the postlarval stage.

The effects of temperature and salinity (excluding 5‰ because only two postlarvae were obtained there) on the number of larval stages are shown in Figures 3 and 4. Sample sizes were unequal, so an approximate method, the analysis of unweighted means (Snedecor, 1956) was employed to indicate significant effects (Table 4). The effect of salinity was not significant, although there appeared to be a slight tendency

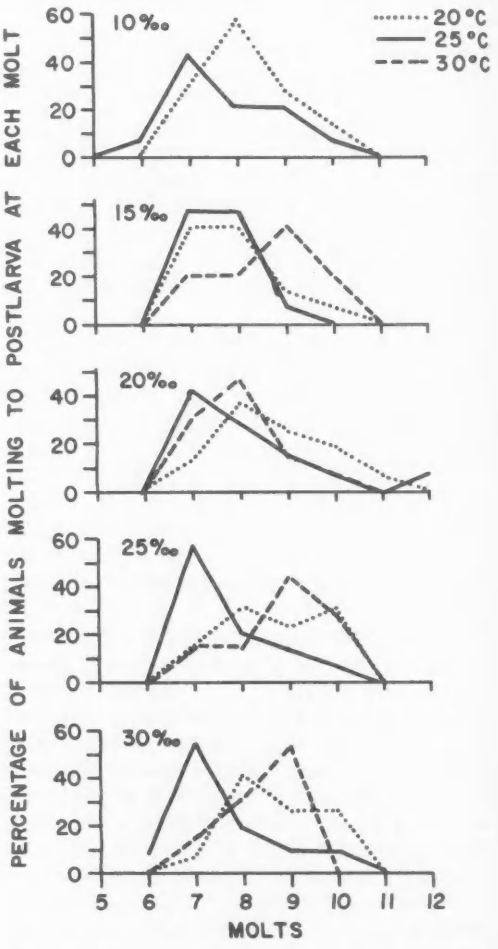

FIGURE 3.—Percentage of animals molting to postlarva at each molt under different conditions of temperature and salinity.

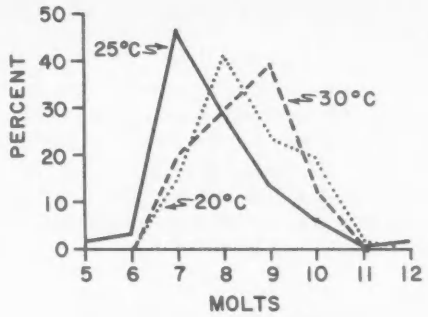

FIGURE 4.—Percentage of animals molting to postlarva at each molt under different temperatures.

for fewer instars in 15‰ than in other salinities. The temperature-salinity interaction also was not significant. However, the influence of temperature was significant at the 1% level, and mean numbers of instars ± one standard deviation were 8.5 ± 1.0 at 20°C, 7.8 ± 1.1 at 25°C, and 8.4 ± 1.0 at 30°C. A multiple mean test showed no difference between the mean numbers of larval instars passed at 20° and 30°C but indicated that animals reared at 25°C passed through significantly fewer instars in larval development.

DISCUSSION

Few previous studies have been concerned with the effects of temperature and salinity on *Palaemonetes* larvae. Sollaud (1919) reared larvae of *P. varians microgenitor* in the laboratory and found, as I did for *P. vulgaris*, that development was retarded at low temperatures and in low salinities and that more instars were passed at the lower than at the more moderate temperature tested. According to Broad and Hubschman (1962), development of larvae of *P. intermedius*, *P. pugio*, and *P. vulgaris* was unaffected by salinity above 20‰, but below 10‰ survival was poor. In the present study, survival in 5‰ was very poor, but in salinities of 10 to 30‰ at low and moderate temperatures (20° and 25°C), survival was high. More recently, Knowlton (1970) conducted a factorial experiment similar to mine, but he used only five larvae in each temperature-salinity combination. Knowlton (1970) found that at 20° and 25°C *P. vulgaris* larvae seemed to tolerate the entire range of salinity tested (15 to 35‰) equally well, with highest survival among larvae reared at 25°C. Lowest survival occurred among larvae reared at 30°C, where no larvae exposed to the low salinities (15 and 20‰) completed development. The results of the present study were fairly similar, except that some larvae survived through metamorphosis at 30°C in all salinities but 5‰. However, Knowlton's (1970) values for mean duration of larval life (37.3 ± 2.0 days at 20°C, 30.7 ± 2.0 days at 25°C, and 31.1 ± 4.3 days at 30°C) were considerably greater than corresponding values in the present study (30.2 ± 3.8 days, 16.6 ± 2.7 days, and 15.7 ± 1.8 days, respectively). Similarly, his values for mean instar duration were greater than values determined here.

The number of larval instars varied from 8 to 16 in Knowlton's (1970) study, while in the present study the observed range was 5 to 12. Knowlton (1965, 1970) also found that the number of larval instars increased with increasing

TABLE 4.—Summary of analysis of variance for differences in number of larval molts for *Palaemonetes vulgaris* larvae at different temperatures and salinities.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*
Total	14	4.0364		
Temperature	2	2.2770	1.1385	10.8017**
Salinity	4	0.5398	0.1349	1.2798 n.s.
Temperature × salinity	8	1.2196	0.1524	1.4459 n.s.
Error	[1]167		[1]0.1054	

** Significant at 1% level. n.s. Not significant.
[1] See Snedecor (1956) for computation of the error mean square in the method of unweighted means.

temperature. In contrast, larvae in my study passed through fewer instars at the moderate temperature (25°C) than at higher or lower temperatures, and at each temperature larvae required fewer molts to reach the postlarval stage in my study than in Knowlton's (1970). Similarly, Ewald (1969) found that *Tozeuma carolinense* larvae passed through fewer instars at 25°C than at 15° and 20°C. He also reported that there were marked differences in the numbers of instars among *T. carolinense* larvae from different populations. Perhaps a similar effect was partially responsible for differences between the numbers of *P. vulgaris* larval instars observed by Knowlton (1970) and by me.

The final zoeal instar was of greater duration than the other instars in both Knowlton's (1970) study and in mine, but the reason for the delay of this molt is not known. However, Hubschman (1963) reported that the X organ-sinus gland complex does not become functional as the primary molt regulator in *Palaemonetes* until after metamorphosis. He suggested that perhaps the rapid larval molting cycle was under the hormonal control of some type of larval molting gland, the existence of which remains speculative. The longer duration of the final zoeal instar thus may reflect transfer of control over molting from some unknown larval molt-regulating mechanism to the X organ-sinus gland complex, or breakdown of the larval regulatory mechanism prior to assumption of molt-regulating function by the X organ-sinus gland complex, or other internal reorganization prior to metamorphosis.

Because of the characteristic variability of temperature and salinity in estuaries, success of a particular decapod species may depend on the ability of the larvae to survive frequent exposure to suboptimal temperature-salinity conditions, to settle and/or metamorphose only under those conditions which are suitable for survival of the adult form, and to remain within, be carried into, or return to a given area to replenish the parental population. The number of larval instars may also be important, since ecdyses are critical periods in larval life, and highest mortality of cultured decapod larvae often occurs then (Ong, 1966; Knowlton, 1970; Roberts, 1971). Reduction of the number of premetamorphic molts thus may increase larval survival. So, considering survival, rate of development, and number of instars, it appears that optimal conditions for larval development of *P. vulgaris* occur at a moderate temperature of about 25°C in salinities of 10 to 30‰. Knowlton (1970) also concluded that a temperature of 25°C was optimal over the salinity range tested (15 to 35‰) in his experiment.

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APPENDIX TABLE 1.--Comparison of survival and developmental rates of Palaemonetes vulgaris larvae reared at different temperatures and salinities.

Temperature (°C)	Salinity (°/oo)	Molt No. 1 Zoea I to zoea II: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Molt No. 2 Zoea II to zoea III: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Molt No. 3 Zoea III to zoea IV: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Molt No. 4 Zoea IV to zoea V: Survival %	Survival No.	Age (days) Mean	Age (days) Range
20	5	11.1	2	4.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	100.0	18	3.0	--	100.0	18	6.5	6-9	88.9	16	9.8	9-12	88.9	16	13.5	12-16
	15	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.1	9-10	100.0	18	12.3	12-17
	20	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
	25	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
	30	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
25	5	72.3	13	2.8	2-7	27.8	5	6.2	4-9	22.2	4	9.8	8-13	22.2	4	11.8	10-15
	10	100.0	18	2.0	--	100.0	18	3.8	3-4	100.0	18	5.8	4-6	100.0	18	7.8	7-8
	15	100.0	18	2.0	--	100.0	18	3.1	3-4	100.0	18	5.1	5-6	100.0	18	7.1	7-8
	20	100.0	18	2.0	--	100.0	18	3.2	3-5	100.0	18	5.2	5-7	100.0	18	7.2	7-9
	25	100.0	18	2.0	--	100.0	18	3.4	3-4	100.0	18	5.3	5-6	100.0	18	7.3	7-8
	30	100.0	18	2.0	--	100.0	18	3.3	3-4	100.0	18	5.3	5-6	88.9	16	7.3	7-9
30	5	11.1	2	2.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.9	4-5	94.5	17	6.9	6-7
	15	94.5	18	2.0	--	88.9	16	3.0	--	83.4	15	4.3	4-5	83.4	15	6.3	6-7
	20	100.0	18	2.0	--	100.0	18	3.0	--	94.5	17	4.1	4-5	94.5	17	6.1	6-7
	25	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.2	4-5	100.0	18	6.1	6-7
	30	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.2	4-5	94.5	17	6.0	--

Temperature (°C)	Salinity (°/oo)	Molt No. 5 Zoea V to zoea VI: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Zoea V to postlarva: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Molt No. 6 Zoea VI to zoea VII: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Zoea VI to postlarva: Survival %	Survival No.	Age (days) Mean	Age (days) Range
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	88.9	16	17.4	16-20	0.0	0	--	--	83.4	15	21.4	20-25	0.0	0	--	--
	15	100.0	18	16.2	15-21	0.0	0	--	--	94.5	17	20.1	18-25	0.0	0	--	--
	20	100.0	18	15.4	15-19	0.0	0	--	--	94.5	17	19.1	18-23	0.0	0	--	--
	25	100.0	18	15.2	15-16	0.0	0	--	--	94.5	17	19.1	18-20	0.0	0	--	--
	30	100.0	18	15.1	15-16	0.0	0	--	--	100.0	18	18.7	18-19	0.0	0	--	--
25	5	16.7	3	12.7	12-13	5.6	1	22.0	--	16.7	3	14.7	14-15	0.0	0	--	--
	10	100.0	18	10.0	9-11	0.0	0	--	--	94.5	17	12.4	11-13	5.6	1	15.0	--
	15	100.0	18	9.2	9-10	0.0	0	--	--	100.0	18	11.2	11-12	0.0	0	--	--
	20	100.0	18	9.2	9-11	0.0	0	--	--	94.5	17	11.1	11-12	0.0	0	--	--
	25	94.5	17	9.4	9-10	0.0	0	--	--	94.5	17	11.5	11-13	0.0	0	--	--
	30	88.9	16	9.3	9-11	0.0	0	--	--	83.4	15	11.2	11-12	5.6	1	15.0	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	94.5	17	9.0	8-11	0.0	0	--	--	66.7	12	10.8	9-11	0.0	0	--	--
	15	66.7	12	8.3	8-9	0.0	0	--	--	55.6	10	10.6	10-11	0.0	0	--	--
	20	88.9	16	8.1	8-9	0.0	0	--	--	83.4	15	10.0	9-11	0.0	0	--	--
	25	100.0	18	7.9	7-9	0.0	0	--	--	94.5	17	9.9	9-11	0.0	0	--	--
	30	94.5	17	7.7	7-8	0.0	0	--	--	88.9	16	9.7	9-10	0.0	0	--	--

Temperature (°C)	Salinity (°/oo)	Molt No. 7 Zoea VII to zoea VIII: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Zoea VII to postlarva: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Molt No. 8 Zoea VIII to zoea IX: Survival %	Survival No.	Age (days) Mean	Age (days) Range	Zoea VIII to postlarva: Survival %	Survival No.	Age (days) Mean	Age (days) Range
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	83.4	15	25.4	24-29	0.0	0	--	--	38.9	7	29.0	28-30	44.5	8	30.9	29-35
	15	50.0	9	23.3	23-24	33.4	6	26.7	24-30	16.7	3	27.3	27-28	33.4	6	28.3	27-30
	20	83.4	15	22.8	22-24	11.1	2	26.0	24-28	44.5	8	26.4	25-27	33.4	6	27.5	27-28
	25	83.4	15	22.9	22-24	11.1	2	25.5	25-26	50.0	9	26.6	25-28	22.2	4	27.5	27-28
	30	94.5	17	22.1	21-23	5.6	1	23.0	--	55.6	10	25.3	24-27	33.4	6	27.2	26-28
25	5	5.6	1	18.0	--	0.0	0	--	--	0.0	0	--	--	5.6	1	21.0	--
	10	50.0	9	14.7	14-16	33.4	6	16.3	14-17	27.8	5	17.4	16-18	16.7	3	17.3	17-18
	15	50.0	9	13.3	13-14	38.9	7	14.6	14-15	5.6	1	15.0	--	38.9	7	17.0	16-18
	20	55.6	10	13.5	13-16	33.4	6	14.0	--	22.2	4	15.3	15-16	22.2	4	16.8	16-17
	25	50.0	9	13.8	13-16	44.5	8	14.8	14-16	33.4	6	16.2	15-18	16.7	3	16.0	--
	30	27.8	5	13.4	13-14	33.4	6	14.2	14-15	16.7	3	16.0	--	11.1	2	16.5	16-17
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	61.2	11	12.9	12-15	0.0	0	--	--	44.5	8	14.6	13-15	0.0	0	--	--
	15	33.4	6	12.7	12-14	5.6	1	15.0	--	22.2	4	14.5	14-16	5.6	1	16.0	--
	20	55.6	10	11.9	11-13	22.2	4	13.0	--	16.7	3	14.0	--	33.4	6	15.0	14-16
	25	66.7	12	11.8	11-13	5.6	1	13.0	--	38.9	7	13.6	13-14	5.6	1	15.0	--
	30	77.8	14	11.6	10-12	11.1	2	13.5	13-14	44.5	8	13.3	12-14	22.2	4	15.3	15-16

APPENDIX TABLE 1.--Comparison of survival and developmental rates of Palaemonetes vulgaris larvae reared at different temperatures and salinities.--Continued.

Temperature (°C)	Salinity (°/oo)	Survival		Age (days)		Survival		Age (days)		Survival		Age (days)		Survival		Age (days)	
		%	No.	Mean	Range	%	No.	Mean	Range	%	No.	Mean	Range	%	No.	Mean	Range
		Molt No. 9								Molt No. 10							
		Zoea IX to zoea X				Zoea IX to postlarva				Zoea X to zoea XI				Zoea X to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	11.1	2	33.0	32-34	22.2	4	34.8	33-36	0.0	0	--	--	11.1	2	38.0	37-39
	15	5.6	1	32.0	--	11.1	2	32.0	--	0.0	0	--	--	5.6	1	37.0	--
	20	22.2	4	30.8	30-31	22.2	4	30.8	30-32	5.6	1	34.0	--	16.7	3	35.0	34-36
	25	27.8	5	29.6	28-31	16.7	3	32.3	31-33	5.6	1	35.0	--	22.2	4	34.0	32-35
	30	27.8	5	28.4	27-29	22.2	4	29.5	28-31	0.0	0	--	--	22.2	4	33.0	31-34
25	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	5.6	1	19.0	--	16.7	3	21.7	20-23	0.0	0	--	--	5.6	1	23.0	--
	15	0.0	0	--	--	5.6	1	18.0	--	0.0	0	--	--	0.0	0	--	--
	20	11.1	2	17.0	--	11.1	2	18.5	18-19	5.6	1	19.0	--	5.6	1	20.0	--
	25	16.7	3	18.7	17-20	11.1	2	19.5	18-21	5.6	1	23.0	--	5.6	1	20.0	--
	30	11.1	2	18.0	--	5.6	1	19.0	--	5.6	1	21.0	--	5.6	1	21.0	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	16.7	3	16.7	16-17	11.1	2	16.5	16-17	5.6	1	19.0	--	5.6	1	19.0	--
	15	11.1	2	17.0	16-18	11.1	2	17.0	--	0.0	0	--	--	5.6	1	21.0	--
	20	5.6	1	16.0	--	11.1	2	16.5	16-17	0.0	0	--	--	5.6	1	18.0	--
	25	11.1	2	15.5	15-16	16.7	3	16.3	16-17	0.0	0	--	--	11.1	2	18.0	17-19
	30	5.6	1	15.0	--	38.9	7	16.3	15-17	0.0	0	--	--	0.0	0	--	--
		Molt No. 11								Molt No. 12							
		Zoea XI to zoea XII				Zoea XI to postlarva				Zoea XII to zoea XIII				Zoea XII to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	0.0	0	--	--	5.6	1	39.0	--	0.0	0	--	--	0.0	0	--	--
	25	5.6	1	39.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
25	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	5.6	1	21.0	--	0.0	0	--	--	0.0	0	--	--	5.6	1	25.0	--
	25	5.6	1	26.0	--	0.0	0	--	--	5.6	1	28.0	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	25	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--

ERYTHROCYTE DEGENERATION IN THE ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS* L.

STUART W. SHERBURNE[1]

ABSTRACT

Cytoplasmic inclusions, associated with erythrocytic degeneration, were found in the circulating blood of herring from Boothbay Harbor, Maine, and from Passamaquoddy Bay at Deer Island, N.B., Canada, in 1969. Except in one instance, when inclusions occurred in herring from water of 2°C, all herring from Boothbay Harbor having inclusions were taken from seawater temperatures of 13.8°C or above. A relationship appears to exist between inclusions in herring erythrocytes and stress factors, especially temperature extremes. At a temperature of 16°C, 96% of a sample of herring were affected with inclusions. Herring sampled at the highest temperature (16°C) were markedly different from all other samples in their blood morphology and had the highest incidence of inclusions. Inclusions were found in the Passamaquoddy Bay area in 2 of the 50 herring sampled from a seawater temperature of 9.8°C, the highest temperature sampled in that area.

Inclusions rarely occurred more than one to a red cell and varied in size from 1.3 to 3.9 μ. In herring containing a high incidence of inclusions, the larger inclusions were usually in the youngest red cells. Cells containing inclusions generally appeared rounded and swollen. Either an abnormally high percentage of up to 90% immature red cells or a low of 1 to 5% immature red cells generally characterized herring containing inclusions.

The blood of herring has been studied at the National Marine Fisheries Service Laboratory at Boothbay Harbor to find physiological indicators of environmental stress that may help us to determine causes of fluctuations in success of year classes. During this investigation I observed inclusion bodies in the cytoplasm of the red cells in many of the herring. In this report I describe these inclusion bodies, their incidence, and the abnormal blood cell morphology associated with these bodies.

Nonspecific cytoplasmic inclusions have been reported in *Fundulus* sp. (Gardner and Yevich, 1969) occurring in wet smears in May and July prior to, and at the beginning of the new breeding season, but not evident in fixed smears. The cytoplasm of erythrocytes from chinook salmon, *Oncorhynchus tshawytscha,* sockeye salmon, *Oncorhynchus nerka,* and adult rainbow trout, *Salmo gairdneri,* contained granular material following fixation procedures (Ridgway, 1956) that the author thought were of mitochondrial origin.

Laird and Bullock (1969) reported finding a distinctive inclusion body formed in the cytoplasm of infected cells associated with piscine erythrocytic necrosis which is responsible for massive red blood cell destruction in *Gadus morhua* from Passamaquoddy Bay. *Liparis atlanticus* from Kent Island, N.B., Canada, and *Myoxocephalus octodecemspinosus* from Portsmouth Harbor, N.H. were lightly infected.

MATERIALS AND METHODS

The 355 herring examined in this study from February through October 1969 consisted of 201 wild herring and 154 captive herring in 12 samples. The herring ranged in length from 12.5 to 30.4 cm and in weight from 10.6 to 214.5 g. The wild herring were taken from four fishermen's catches between central Maine and Canada. Three categories of herring are considered

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in this report: 1) long-term captive herring held 6 months before sampling began in February and terminated in June when the supply of test fish was exhausted, 2) short-term captives which consisted of herring held 2 weeks before being bled, and 3) wild herring that were taken when available. The captive herring were held in seawater which was pumped from the ocean through the tanks and which approximated the temperature of natural seawater. The water temperature was recorded at the site of capture in each instance.

A blood sample was taken from the heart of each herring and preserved in a modified Alsever's solution for serological studies; a microhematocrit was determined and a morphology slide made for each herring. The herring were measured for total length, weighed, sexed, marked, and frozen for reference. All herring were examined for gross parasitism.

The hematocrits and morphology slides were made of blood taken by direct heart puncture with a heparinized 75 mm × 1.3-1.5 mm outside diameter capillary tube. A small drop of blood from the tube was placed on a microscope slide, the tube sealed with plastic clay, and the smear made. The tubes were centrifuged in a microhematocrit centrifuge for 3½ min at 11,000 rpm and read in a microcapillary reader. Slides were air-dried and stained by either the Wright's or Wright-Giemsa staining method. Distilled water was used as a diluent for the Wright's and Giemsa stains. Cells were examined under oil immersion and photographed at 800 and 1250 powers. Hematocrits were measured as the volume percent of packed red cells to the total blood column. (The term "hematocrit" is used in this paper, although Widmark (1970) has suggested the term be replaced with "packed cell volume").

I classify herring erythrocytes according to the stage of development in the peripheral blood as erythroblasts, early polychromatics, middle polychromatics, late polychromatics or mature cells, depending upon their size and the amount of polychromasia present. These stages are described in Table 1. Reticulocytes cannot be identified readily without vital staining so are not included in Table 1. There are variations in individual herring in the size and shape between and within cell stages and the amount of polychromasia present is the best indicator as to the series to which the cell belongs.

RESULTS

The sample source, date of sampling, incidence of inclusion bodies, mean length, standard deviation and range in lengths, mean weight,

TABLE 1.—The developmental stages and the average size of erythrocytes in the peripheral blood of wild herring.

Stage	Description	Cell measurements[1] (microns)	
		Cytosome	Nucleus
Erythroblast	Round, slightly larger cell than the early polychromatic. Has a dark blue staining cytoplasm with lightly stained spaces. The round purple-red staining nucleus takes up most of the cell. Erythroblasts are scarce in normal samples.	7.8 × 7.3	5.9 × 6.2
Early polychromatic	The smallest immature red cell that is normally seen in any quantity. Has a light blue to gray staining cytoplasm and appears round. The nucleus takes up most of the cell.	7.8 × 7.1	4.6 × 3.3
Middle polychromatic	Round to slightly oval cell with a gray to light gray-orange staining cytoplasm. Cell is larger than the early polychromatic.	9.5 × 7.0	4.8 × 3.0
Late polychromatic	Slightly oval, has a larger cytoplasm and a smaller nucleus than the middle polychromatic. The cytoplasm appears light orange-yellow.	10.0 × 7.7	4.6 × 2.9
Mature erythrocyte	Oval, has a slightly larger cytoplasm and a slightly smaller nucleus than the late polychromatic. The cytoplasm appears orange-yellow to reddish. Late polychromatic and mature cells have essentially the same appearance with Wright's stain.	10.3 × 7.7	4.2 × 2.8

[1] Measurements based on 25 cells in each stage from a normal wild herring in March.

TABLE 2.—The occurrence of inclusion bodies in the cytoplasm of herring erythrocytes, 25 February-30 October 1969.

Sample source and category[1]	Date	Incidence in sample	Percent incidence	Water temp. (°C)	Mean length, SD, and range of sample (cm)	Mean weight, SD and range of sample (g)
Long-term captives	25 Feb.	0/25	0.0	1.3	15.3 ± 0.79(14.0-17.2)	20.2 ± 4.3(14.1- 29.0)
Wild, Sheepscot River, Boothbay Harbor	13 Mar.	1/35	2.9	2.0	16.4 ± 2.0 (13.5-19.0)	26.2 ± 9.7(14.0- 42.0)
Long-term captives	24 Mar.	0/25	0.0	3.3	16.0 ± 0.99(13.2-17.5)	20.7 ± 4.5(10.6- 29.4)
Long-term captives	21 Apr.	0/20	0.0	4.9	16.3 ± 0.99(14.3-17.7)	23.0 ± 5.0(14.9- 33.1)
Wild, Eastport, Maine	10 June	0/40	0.0	7.7	22.2 ± 3.0 (14.5-30.4)	80.3 ± 41.3(18.0-214.5)
Long-term captives	23 June	2/12	16.7	15.2	16.2 ± 1.4 (13.1-18.0)	22.8 ± 5.8(14.1- 34.7)
Wild, Spruce Point, Boothbay Harbor	8 July	5/76	6.6	13.8	15.5 ± 1.4 (12.5-18.5)	23.7 ± 6.6(12.8- 43.4)
Wild, Deer Island, N.B., Canada	16 July	2/50	4.0	9.8	21.0 ± 1.9 (13.9-25.2)	81.0 ± 21.1(13.6-133.0)
Short-term captives	22 July	24/25	96.0	16.0	16.0 ± 1.2 (14.4-18.0)	25.3 ± 5.7(17.6- 36.4)
Short-term captives	21 Aug.	3/25	12.0	14.0	16.1 ± 1.3 (13.2-18.6)	22.1 ± 6.2(11.7- 40.9)
Short-term captives	25 Aug.	0/10	0.0	15.5	17.7 ± 1.2 (15.3-20.0)	29.9 ± 7.4(18.5- 48.1)
Short term captives	30 Oct.	0/12	0.0	9.2	16.2 ± 1.1 (15.1-19.0)	20.6 ± 4.2(16.3- 27.6)

[1] Long-term captives—Boothbay Harbor herring held 5 months before being bled.
Short-term captives—herring from wild 8 July sample held 2 weeks before being bled.

and standard deviation and range in weights of all herring included in this study are given in Table 2.

DESCRIPTION OF INCLUSION BODIES

The inclusions are round, granular, intracytoplasmic and appear acidophilic with Wright's stain. The inclusions generally occur singly in the affected cells and vary in size with the largest inclusions usually in the youngest cells. A few red cells contained two inclusions. The bodies characteristically range in size from 2.3 to 3.3 μ in early polychromatics, 1.7 to 1.9 μ in middle polychromatics, and 1.3 to 1.6 μ in late polychromatics and mature erythrocytes. The inclusions vary from bright red to reddish-purple in contrast with the blue-gray cytoplasm of the young cells and the dull orange-yellow cytoplasm of the mature cells. Many inclusions have a dark-purple periphery with a light central zone; other inclusions are the same color throughout. Some of the larger inclusions appear to have at least four small, dense-staining particles within or along the periphery of the inclusion.

Inclusions were not found outside the red cells, nor were inclusions observed in any white cells of the 355 herring examined in this study.

MORPHOLOGY

Wild herring that did not contain inclusions ranged from 3 to 35% with an average of 20% immature erythrocytes, while captive herring without inclusions ranged from 2 to 25% with an average of 14% immature erythrocytes in their peripheral blood.

Two types of morphology usually characterized the blood of herring that contained inclusions: either upward to 90% immature red cells or a low of 1 to 5% immature red cells. The single herring with inclusions in March had the highest percentage of immature erythrocytes I had found in wild herring to that date. Eighty percent of the red cells were immature, with 12% of the immature and 90% of the mature cells affected with inclusions. Erythroblasts, rare in a normal blood sample, were abundant on this slide. The inclusions occurred singly in the cytoplasm and varied in size; the largest were in the youngest cells. The bodies ranged in size from 2.3 to 3.1 μ in early polychromatics, 1.7 to 1.9 μ in middle polychromatics, and 1.3 to 1.6 μ in late polychromatics and mature erythrocytes. The nucleus of the affected cells exhibited vacuolization and pyknosis. Abnormally large immature red cells (macrocytes) were evident with atypical cells present in all developmental stages (Figure 1). The remaining 34 herring in the sample had normal red cell morphology (Figure 2).

Inclusions first appeared in long-term captive herring in June in 2 out of 12 specimens. These two herring had the lowest hematocrits of the sample. The blood morphology of the two affected herring differed. One herring had 60%

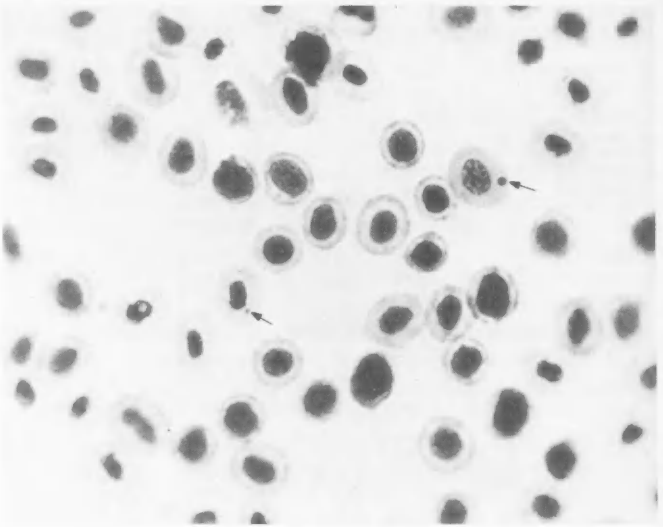

FIGURE 1.—13 March 1969. Photomicrograph of wild herring blood showing macrocytosis of the young cells. Early polychromatics are prevalent. Arrows point to an inclusion in a middle polychromatic and in a mature red cell.

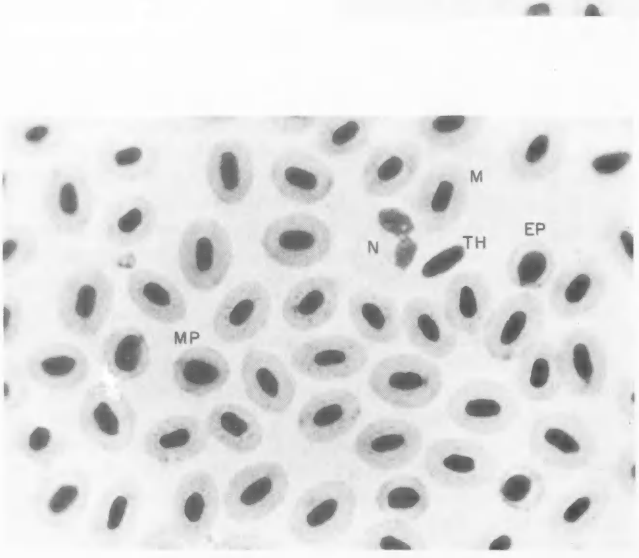

FIGURE 2.—13 March 1969. Photomicrograph of normal wild herring blood showing the absence of inclusions.

EP — early polychromatic erythrocyte
MP — middle polychromatic erythrocyte
M — mature erythrocyte
N — neutrophil
Th — thrombocyte

immature red cells with inclusions found in only 6% of the mature red cells; the other affected herring had 12% immature red cells with inclusions in 50% of the immature and 20% of the mature cells.

Nearly 7% (5/76) of the wild herring sampled on 8 July from Boothbay Harbor contained inclusions, and a few cells in several herring contained two inclusions. Four of the five affected herring contained over 70% immature red cells, the other 15%. Both abnormally large and small erythrocytes and many disintegrated cells were present. Anisopoikilocytosis (abnormal cell sizes and shapes) of all red cell developmental stages was evident. The nuclei of many affected erythrocytes contained two or

three large vacuoles. The affected mature cells were rounded instead of the usual oval (Figure 3); a typical rounded mature cell measured 10.1 × 9.4 μ for the cytosome, 3.7 × 3.4 μ for the nucleus, and 1.2 × 1.5 μ for the inclusion body. Vacuolization of the cytoplasm was evident in many red cells. Inclusions were present in some microcytic mature erythrocytes as small as 4 × 4 μ for the cytosome (less than one-half normal size). Inclusions in a few early polychromatics were larger than usual. One of the largest inclusions in a young cell was nearly as large as the cell nucleus—the cytosome measured 9.2 × 8.0 μ, the nucleus 4.7 × 3.7 μ, and the inclusion 3.9 × 3.6 μ (Figure 4). Otherwise inclusions in the wild herring of March and July were of the same size.

A relationship appears to exist in the occurrence of inclusions and abnormal red cell morphology with temperature extremes. The short-term captive herring sampled on 22 July at 16°C, the highest temperature at which samples were taken, were markedly different from all other samples in their morphology and incidence of inclusions. Ninety-six percent (24/25) of the herring had inclusions, and of those over half had inclusions in at least 90% of their red cells. A majority of the smears in this sample showed 5% or less intact immature red cells. Anucleated "balloon" cells were evident in all smears in this sample, some smears had up to 50% of these cells (Figure 5). The balloon cells appear pale red with Wright's stain, are similar in size, and range from 9.4 × 9.4 μ to 10.9 × 10.9 μ. Some of the cells appear to show diffusion of nuclear material into the cytoplasm. The smears with the greatest incidence of inclusions generally had the most balloon cells. The most heavily affected herring from the 8 July sample also showed these cells. In the smear free of inclusions a few balloon cells were seen, the intact cells appeared normal and 10% immature red cells were present (Figure 6). Such balloon cells are seen in apparently normal blood samples only occasionally and in very low frequency.

The short-term captive herring sampled on 21 August at 14°C showed a substantial decrease in inclusions with 12% of the sample affected, but many nonaffected fish had abnormal cells (Figure 7). Higher than normal seawater temperatures of up to 20.5°C (68.9°F) during August may account for the abnormal cells in herring without inclusions.

Inclusions were found in 2 of the 50 herring

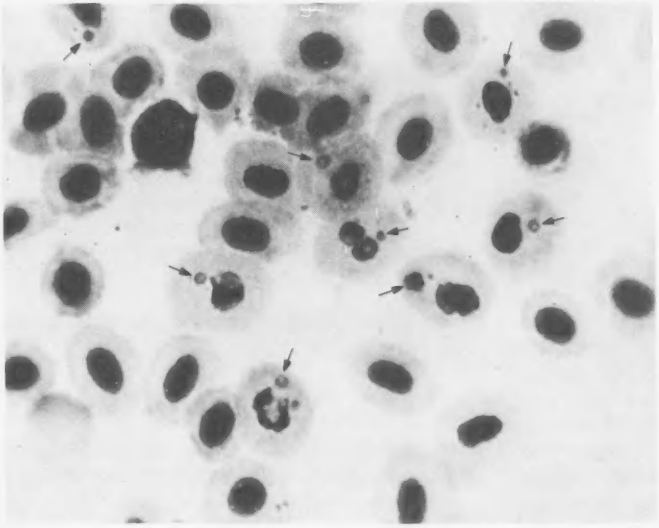

FIGURE 3.—8 July 1969. Photomicrograph of wild herring blood showing intracytoplasmic inclusions associated with nuclear degeneration and a ballooning of the red cells.

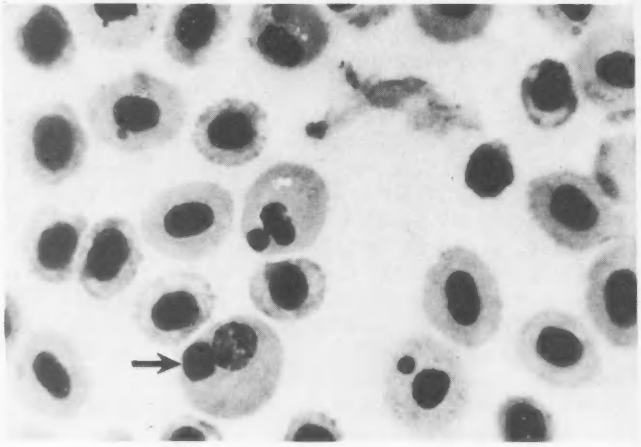

FIGURE 4.—8 July 1969. Photomicrograph of wild herring blood showing one of the largest inclusions seen in this study. The inclusion measures 3.9 × 3.6 μ, the cell nucleus 4.7 × 3.7 μ, and the cytosome 9.2 × 8.0 μ.

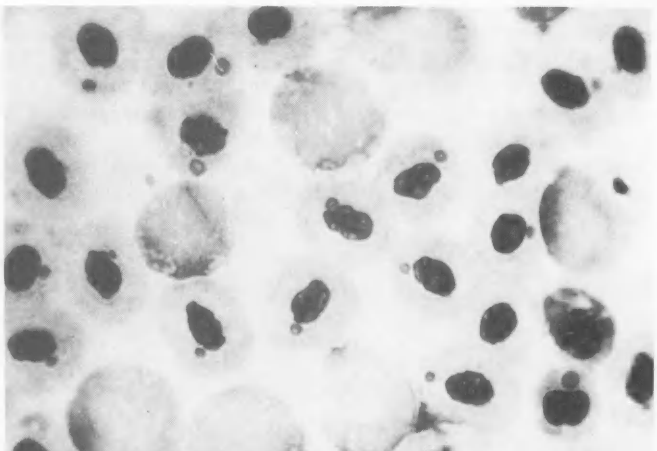

FIGURE 5.—22 July 1969. Photomicrograph of herring blood from a short-term captive, 2 weeks after placing wild fish from the 8 July sample in the tanks, showing nearly all of the red cells affected with inclusions, abnormal nuclei, and anucleated "balloon" cells.

sampled on 16 July from Deer Island, N.B., Canada. One herring had 25% immature red cells with inclusions in less than 1% of the immatures; the other affected herring had 90% immature red cells with inclusions in 1% of the immature and 90% of the mature red cells. The morphology and size of inclusions were similar to that of the 8 July samples from Boothbay Harbor. The smear with the greatest incidence of inclusions showed approximately 20% balloon cells.

HEMATOCRITS

The hematocrit mean, standard deviation, and range for each sample and hematocrit values of the males and females in each sample are shown in Table 3. The lowest hematocrit for an indi-

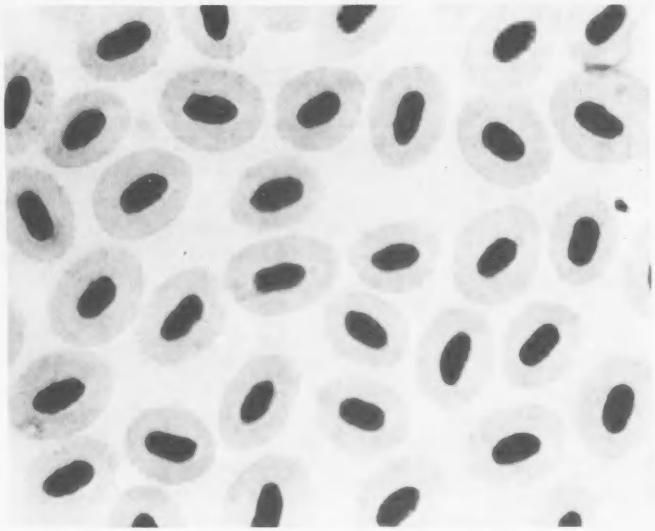

FIGURE 6.—22 July 1969. Photomicrograph of normal red cells from the only herring not affected with inclusions from a sample of 25 short-term captives.

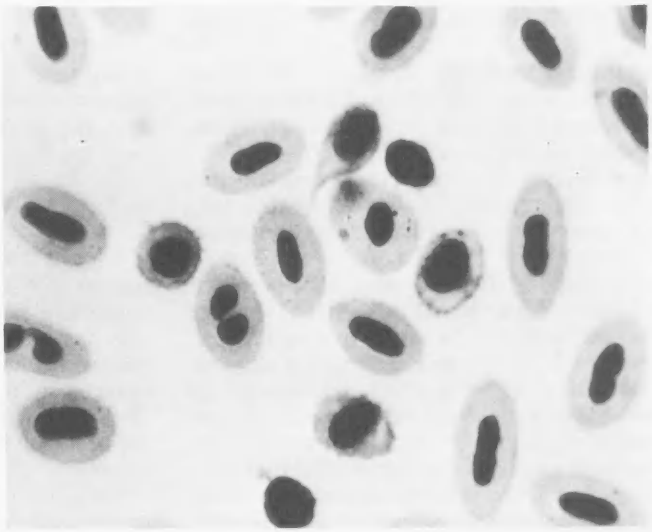

FIGURE 7.—21 August 1969. Photomicrograph of abnormal cells in short-term captive herring. Higher than normal natural seawater temperatures of up to 20.5°C (68.9°F) during August may account for the abnormal cells in herring not affected with inclusions. This herring had one of the lowest hematocrits of the sample (21 volumes percent); the scarcity of cells on the slide reflects this finding.

vidual herring in this study was 17 volumes percent; the highest, 54.5 volumes percent. The lowest mean hematocrit for a sample was 28.7 volumes percent for the long-term captives in March; the highest mean hematocrit was 41.4 volumes percent for a sample of wild herring in July. The *t*-test analysis revealed no significant differences in hematocrit values between sexes in these immature herring.

A consistent decrease is evident in the mean hematocrit values of the wild herring from the time they were placed in captivity on 8 July

TABLE 3.—Hematocrits of herring samples and sexes within each sample, 25 February-30 October 1969.

Date	Water temp. (°C)	Herring sampled (Number)	Hematocrits of samples		Mean hematocrits of:		Standard deviation
			Range (vol %)	Mean (vol %)	Males (vol %)	Females (vol %)	
Long-term captives[1]:							
25 Feb.	1.3	23	22.5-38.0	29.7			4.1
24 Mar.	3.3	25	22.5-36.0	28.7			3.6
21 Apr.	4.9	20	23.0-42.5	31.2			4.3
23 June	15.2	5	22.0-42.0		34.9		7.8
		7	22.5-43.5			36.3	7.9
		12	22.0-43.5	35.7			7.5
Wild, Spruce Point, Boothbay Harbor:							
8 July	13.8	27	27.0-54.5		42.2		6.0
		49	31.0-49.5			40.9	4.5
		76	27.0-54.5	41.4			5.0
Short-term captives[2]:							
22 July	16.0	13	25.0-47.0		40.5		6.1
		12	34.0-53.0			39.6	5.4
		25	25.0-53.0	40.1			5.7
21 Aug.	14.0	12	21.0-46.5		36.5		6.9
		13	17.0-52.5			35.4	8.9
		25	17.0-52.5	36.0			7.9
25 Aug.	15.5	4	23.0-31.5		28.6		3.8
		6	24.0-39.0			33.5	6.2
		10	23.0-39.0	31.6			5.7
30 Oct.	9.2	12	23.0-39.0	30.3			5.2

[1] Boothbay Harbor herring held 6 months before being bled.
[2] Herring from the wild 8 July sample held 2 weeks before being bled.

until the final bleeding on 30 October. Seawater temperatures from 30 July to 22 August were higher than normal with the captive herring exposed to temperatures of up to 20.5°C (68.9°F). The physiology of the short-term captives was undoubtedly affected as evidenced by the many disintegrated red cells and abnormal cell types seen in the blood of herring not containing inclusion bodies. The marked variation in cell sizes and shapes, teardrop cells and bizarre forms are rarely seen in normal herring blood.

In 1965 I noted a close correlation between hematocrit values in herring and hemoglobin concentrations measured by the cyanmethemoglobin method. I have found no references on hematocrit values of the Atlantic herring, so I include the relations I found between hematocrit values and hemoglobin concentrations here. The herring sampled in 1965 were long-term captive herring 12.7-25.4 cm in length. Hematocrits were taken as described in the present study. Blood for hemoglobin measurements was obtained from the heart and placed in a small test tube to which a drop of liquid heparin had been added. Hemoglobins were measured as grams per 100 ml. Regression analysis gave a correlation coefficient of 0.9333. The regression line with the confidence limits of Y at the 0.05 level are shown in Figure 8.

DISCUSSION

Boyar (1962) reported that mature red cells constitute 97-100% of all blood cells in herring blood, and the immature red cells plus white cells made up less than 3% of the total cells in the herring he examined. However, I found an average of 20% immature erythrocytes in the blood of normal wild herring and 14% immature erythrocytes in the blood of normal captive herring.

The occurrence of cytoplasmic inclusions had no apparent relationship to sex, length, weight, or hematocrits, nor did herring with inclusions show, on cursory examination, more than the usual parasites observed in samples without inclusions. The occurrence of inclusions is associated with other hematological abnormalities in the peripheral blood including upward to 90% immature red cells or a low of 1 to 5% immature

red cells in contrast to the 20% immature red cells normal for wild herring; microcytic erythrocytes less than one-half normal size; and varying degrees of anisocytosis and poikilocytosis. The affected red cells have some characteristics of piscine erythrocytic necrosis (PEN) as described by Laird and Bullock (1969), in a cod, *Gadus morhua*, from Passamaquoddy Bay. These authors associated the PEN in cod with viruslike particles. Walker (1971; pers. comm., July 1972) has confirmed the viral nature of PEN in cod by electron microscopy. He also confirmed the correlation of nuclear lesions as described by Laird and Bullock with the presence of cytoplasmic viroplasm and virions. Although I believe the inclusion bodies in herring can be explained as a physiological response to environmental stress, the possibility of their viral nature has not been ruled out and requires further investigation.

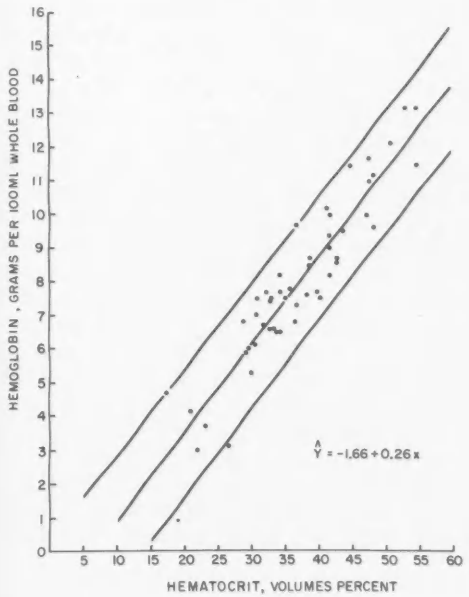

FIGURE 8.—Relation of hematocrit values to hemoglobin concentrations in captive herring during late winter, 1965.

A relationship appears to exist between inclusions in herring erythrocytes and stress factors, especially temperature extremes. Except in one instance when inclusions occurred in herring from water of 2°C, all herring from Boothbay Harbor (lat 43°50′N, long 69°40′W) having inclusions were taken from seawater temperatures of 13.8°C or above. At a temperature of 16°C, 96% of a sample of herring were affected with inclusions. Inclusions were found in 2 of 90 herring sampled from the Passamaquoddy Bay area (lat 45°00′N, long 67°00′W). These herring were taken from a seawater temperature of 9.8°C, the highest temperature sampled in that area. During the months of June and July water temperatures in the Passamaquoddy Bay area have, over a number of years, averaged approximately 4°C lower than in the Boothbay Harbor area (Colton and Stoddard, 1972).

The incidence of inclusions within a population can change rapidly, apparently with changing environmental conditions, and they are capable of affecting a high percentage of herring within a population in a very short time. As an example, the wild herring on 8 July from Boothbay Harbor had a 6.6% incidence of inclusions (5/76); however, 2 weeks after herring from this population were placed in the laboratory tanks, 96% of the herring sampled (24/25) were affected with inclusions, and over 90% of the red cells in individual herring contained these bodies.

These bodies, associated with erythrocytic degeneration characterized by necrotic nuclei, a ballooning degeneration of the red cells and the appearance of unusual cells in the blood, may be indicative of stress situations for immature herring in the wild. If the stress factors causing these inclusion bodies affect enough herring, they could conceivably have an adverse affect on the population structure endemic to certain areas. The erythrocytic degeneration found in herring may be due to a viral infection as described in other fishes by Laird and Bullock (1969) and confirmed by Walker (1971). The occurrence of such a viral infection in epidemic frequency would certainly be no less important to our understanding of fluctuations in abundance of herring populations.

ACKNOWLEDGMENTS

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FOOD OF TUNAS AND DOLPHINS (PISCES: SCOMBRIDAE AND CORYPHAENIDAE) WITH EMPHASIS ON THE DISTRIBUTION AND BIOLOGY OF THEIR PREY *STOLEPHORUS BUCCANEERI* (ENGRAULIDAE)

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ABSTRACT

The results of examining the stomach contents of skipjack tuna (*Katsuwonus pelamis*), bigeye tuna (*Thunnus obesus*), yellowfin tuna (*Thunnus albacares*), kawakawa (*Euthynnus affinis*), common dolphin (*Coryphaena hippurus*), and the little dolphin (*Coryphaena equiselis*) caught by live bait pole-and-line fishing and trolling in the equatorial eastern Pacific and around the Samoa Islands are presented. Fishes, crustaceans, and molluscs were found to be important food items. The presence of the anchovy, *Stolephorus buccaneeri*, among the stomach contents was of particular interest, and information gained on their distribution, size frequency, fecundity, and food habits is presented.

This report is based mainly on observations and stomach sample collections that were made during *Charles H. Gilbert* cruise 116 to the equatorial eastern Pacific in October-November 1969 (Hida, 1970a) and cruise 117 to the Samoa Islands in February-April 1970 (Hida, 1970b). In this study, *Stolephorus buccaneeri* was first found in the stomach contents of bigeye and skipjack tunas caught in the equatorial eastern Pacific and again in the stomach contents of tunas caught around the Samoa Islands. Since there has been no food study made of tunas and dolphins from these areas and very few reports on the distribution and biology of *S. buccaneeri*, it is the intent of this paper to (1) describe the food items of the tunas and dolphins caught in these two geographically distant and environmentally diverse—oceanic versus insular—areas, (2) extend the known distributional range of *S. buccaneeri*, (3) report on biological information obtained from the anchovy specimens. *Charles H. Gilbert* is a U.S. Department of Commerce, NOAA research vessel assigned to the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service. Objectives of the cruises were to assess the distribution and abundance of surface swimming tunas, to tag and release skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) for migration and growth studies, and to collect blood samples of these tunas for subpopulation studies. Tunas and dolphins were caught by live bait pole-and-line fishing and by trolling. Threadfin shad, *Dorosoma petenense*, were transported from Honolulu in baitwells on both cruises and used as chum for the fishing operation. It was the exclusive baitfish used on cruise 116, while on cruise 117 supplementary baitfishes, mostly sardines, *Sardinella melanura* and *Herklotsichthys punctatus*, and a mackerel, *Rastrelliger kanagurta*, were caught in Pago Pago Harbor and used. Since anchovies were not used as live bait on either cruise, the occurrence of *S. buccaneeri* in the stomachs of the tunas examined indicates that this species is a natural food item in this area.

Many studies have been made on the food and feeding habits of tunas in the Pacific. Ronquillo (1953) examined the stomach contents of yellowfin tuna, skipjack tuna, kawakawa (*Euthynnus affinis*), and the common dolphin (*Coryphaena hippurus*) caught in Philippine seas.

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He found that juvenile fish, especially the acronurus larvae of Acanthuridae, were most important in their diet. Also of importance were members of the fish families Trichiuridae, Scombridae, Triacanthidae, Holocentridae, Balistidae, and Monacanthidae, and invertebrates such as squids, larval and juvenile stomatopods, larval crabs and shrimp. Hotta and Ogawa (1955) examined the stomach contents of skipjack tuna caught to the east and south of the main Japanese islands and reported that Scombridae, Engraulidae, Exocoetidae, and Holocentridae were major dietary items. Important invertebrates included squids, crab larvae, euphausiids, and shrimp. Alverson (1963) examined the stomach contents of skipjack and yellowfin tunas caught in the eastern tropical Pacific. He found euphausiids to be the main food items for skipjack tuna, followed by Gonostomatidae, Exocoetidae, and the "red crab," *Pleuroncodes planipes*; and for yellowfin tuna, the "red crab," the swimming crab (Portunidae), Thunnidae, Ostraciidae, Exocoetidae, and Tetraodontidae. Waldron and King (1963) studied the stomach contents of skipjack tuna taken around the Hawaiian, Line, and Phoenix Islands and found that common dietary items were Gempylidae, Scombridae, Mullidae, Chaetodontidae, and Holocentridae. Larval and juvenile skipjack tuna, stomatopod larvae, shrimp, and crab megalops were also important. E. Nakamura (1965), upon examination of the stomach contents of skipjack tuna from the Marquesas and Tuamotu Islands, reported that scombrids, with skipjack tuna constituting a high percentage, were common food items. Serranidae, Lutjanidae, and Gempylidae were of importance as were stomatopods, crab megalops, and squids. It was concluded by Hotta and Ogawa (1955) that the tunas were nonselective in their feeding habits and ate whatever was available in the area.

Although these previous observations covered broad areas of the Pacific, no mention was made of any anchovy that may have been *S. buccaneeri* occurring in the stomach contents. An exception is a report by H. Nakamura (1936) on the food of yellowfin tuna caught in the Celebes Sea that mentioned an anchovy as one of the common food items. The area in which he found tunas containing the anchovy, the frequency of occurrence of the anchovy in tuna stomachs, and the numbers in which it occurred lead me to believe that it may have been *S. buccaneeri*.

METHODS

The stomachs of the troll and pole-and-line caught fish were removed after they were measured and sexed. Stomachs that appeared empty and those of most male tunas were examined in the field and their contents recorded. The rest were placed in muslin bags and preserved in 10% Formalin.[2] One of the objectives of the cruises was to collect 50 skipjack tuna and/or 50 yellowfin tuna blood samples from each school. Therefore, there were four occasions on which 50 stomach samples per school were collected.

In the laboratory, counts were made of the organisms in the stomachs whenever possible. Many of the partially digested fishes were identified by their vertebrae which were prepared by teasing away the muscles when necessary and staining with alizarin red. Skipjack tuna remains were identifiable by skeletons. Enough of the external characters of the anchovy usually remained for identification. Most of the other fishes were identifiable only to family. The stomach contents of the anchovy, which included many crustaceans, were identified by staining the organisms with methylene blue. Many of the copepods were identified to species but other invertebrates were identifiable only to major groups such as the Chaetognatha, Amphipoda, and shrimp.

STOMACH CONTENTS

EQUATORIAL EASTERN PACIFIC

The results of examining 268 skipjack tuna, 44 bigeye tuna (*Thunnus obesus*), 45 yellowfin tuna, 2 common dolphin, and 7 little dolphin (*Coryphaena equiselis*) caught on cruise 116 of the *Charles H. Gilbert* are presented in Table 1. The presence of *S. buccaneeri* in the stomach

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Frequency occurrence of organisms in the stomachs of 268 skipjack tuna, 44 bigeye tuna, 45 yellowfin tuna, and 9 dolphin (2 common and 7 little) examined from cruise 116 of the *Charles H. Gilbert*.

Food items	Predators							
	Skipjack tuna		Bigeye tuna		Yellowfin tuna		Dolphin	
	No.	%	*No.*	%	*No.*	%	*No.*	%
Fishes:								
Alepisauridae	2	0.7	--	--	--	--	--	--
Bramidae	3	1.1	1	2.3	1	2.2	--	--
Chaetodontidae	--	--	1	2.3	--	--	--	--
Diodontidae	1	0.4	--	--	--	--	--	--
Engraulidae:								
Stolephorus buccaneeri	35	13.1	20	45.4	--	--	--	--
Exocoetidae	3	1.1	--	--	1	2.2	3	33.3
Gempylidae	4	1.5	4	9.1	4	8.9	--	--
Nomeidae	--	--	1	2.3	1	2.2	--	--
Scombridae:								
Auxis rochei	1	0.4	--	--	--	--	--	--
Katsuwonus pelamis	5	1.9	--	--	--	--	--	--
Sternoptychidae	--	--	1	2.3	--	--	--	--
Zeidae	--	--	1	2.3	--	--	--	--
Unidentified	9	3.4	1	2.3	7	15.6	2	22.2
Chum	100	37.3	20	45.4	22	48.9	--	--
Crustacea:								
Amphipoda	2	0.7	--	--	2	4.4	--	--
Euphausiacea	1	0.4	--	--	--	--	--	--
Shrimp	2	0.7	1	2.3	--	--	--	--
Mollusca:								
Argonauta	6	2.2	--	--	1	2.2	--	--
Heteropoda	1	0.4	--	--	3	6.7	--	--
Squids	22	8.2	6	13.6	8	17.8	2	22.2
Chaetognatha	1	0.4	--	--	--	--	--	--
Stomach empty	136	50.7	15	34.1	17	37.8	5	55.6

contents of 13.1% of the skipjack tuna and 45.4% of the bigeye tuna examined was of particular interest. Of the invertebrates, squids were most frequently found in the contents. Many of the stomachs examined were empty.

This study revealed that only a few varieties of organisms were eaten in the oceanic environment, which contrasted markedly with Ronquillo's (1953) work showing a great diversity of organisms eaten in an environment influenced by land. The fact that *S. buccaneeri* was found only in the stomachs of tunas from two schools that were close to each other suggests that it was not widespread in this area.

SAMOA ISLANDS

Table 2 shows the results of examining 205 skipjack tuna, 23 kawakawa, 24 yellowfin tuna, and 1 common dolphin which were caught on cruise 117 of the *Charles H. Gilbert*. *S. buccaneeri* occurred very frequently in the stomachs examined. Other fishes occurring frequently belonged to the families Acanthuridae and Holocentridae. Stomatopod larvae, of the invertebrates, occurred most frequently in the contents. Many of the stomachs examined were empty.

The variety of organisms eaten around the Samoa Islands was limited. However, a comparison of the studies shows a greater diversity ingested around Samoa than in the equatorial eastern Pacific, probably because of the proximity to the islands. The distribution of *S. buccaneeri* was found to be widespread in this area. Their frequency of occurrence in the stomachs suggested that they were an important forage for the tunas and dolphins here.

TABLE 2.—Frequency occurrence of organisms in the stomachs of 205 skipjack tuna, 23 kawakawa, 24 yellowfin tuna and 1 common dolphin, examined from cruise 117 of the *Charles H. Gilbert.*

Food items	Predators							
	Skipjack tuna		Bigeye tuna		Yellowfin tuna		Common dolphin	
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Fishes:								
Acanthuridae	45	22.0	1	4.3	4	16.7	--	--
Balistidae	13	6.3	2	8.7	1	4.2	--	--
Bramidae	--	--	--	--	1	4.2	--	--
Carangidae	3	1.5	--	--	--	--	--	--
Chaetodontidae	11	5.4	--	--	1	4.2	--	--
Dactylopteridae	1	0.5	--	--	--	--	--	--
Engraulidae:								
Stolephorus buccaneeri	38	18.5	4	17.4	6	25.0	1	100
Exocoetidae	5	2.4	--	--	--	--	--	--
Gempylidae	13	6.3	--	--	--	--	--	--
Holocentridae	61	29.8	2	8.7	2	8.3	--	--
Molidae	1	0.5	--	--	--	--	--	--
Monacanthidae	3	1.5	1	4.3	--	--	1	100
Mullidae	2	1.0	--	--	--	--	--	--
Ostraciidae	1	0.5	--	--	--	--	--	--
Pomacentridae	--	--	--	--	1	4.2	--	--
Scombridae:								
Katsuwonus pelamis	19	9.3	--	--	--	--	--	--
Unidentified	8	3.9	--	--	--	--	--	--
Siganidae	8	3.9	--	--	--	--	--	--
Synodontidae (?)	6	2.9	--	--	--	--	--	--
Tetraodontidae	2	1.0	--	--	--	--	--	--
Chum	66	32.2	--	--	--	--	--	--
Unidentified	36	17.6	2	8.7	2	8.3	1	100
Crustacea:								
Amphipoda:								
Phronima sp.	--	--	--	--	1	4.2	--	--
Crab megalops	2	1.0	2	8.7	--	--	--	--
Phyllosoma larvae	1	0.5	--	--	--	--	--	--
Shrimp	--	--	1	4.3	--	--	--	--
Stomatopod larvae	7	3.4	3	13.0	1	4.2	--	--
Mollusca:								
Squids	20	9.8	--	--	1	4.2	--	--
Stomach empty	64	31.0	14	60.8	10	41.7	--	--

NOTES ON *STOLEPHORUS BUCCANEERI*

DISTRIBUTION

Strasburg (1960) described *S. buccaneeri* from Hawaii and proposed the common name, roundhead. His holotype was a specimen taken in a nearshore bait seine haul close to Lehua Island. He also found a few specimens in the stomach contents of kawakawa caught about a mile offshore from Oahu. Matsui (1963) found this species in the bait samples he obtained around the island of Maui.

The abundance of *S. buccaneeri* in Hawaiian waters is not known. This is largely because the Hawaiian skipjack tuna fishermen use the anchovy, *Stolephorus purpureus*, as their principal baitfish. These two fish are almost identical and therefore difficult to distinguish from one another. Anchovies regurgitated on deck and found in the stomach contents of tunas are assumed to be their baitfish. At times, however, Hawaiian skipjack tuna fishermen have reported seeing skipjack tuna feeding on what they refer to as "offshore nehu" (liberal translation of the Japanese term used), which more than likely is *S. buccaneeri*. The distribution of *S. purpureus* is inshore while that of the *S. buccaneeri* seems to be generally offshore. It is therefore proposed that another common name of *S. buccaneeri* might be offshore nehu.

Besides Hawaii, Whitehead (1967) gave the distribution of the *S. buccaneeri* as the Red Sea,

Persian Gulf, Comoro Islands, east coast of Africa, Formosa, Hong Kong, Japan, the Philippines, Palau, southern India, and Singapore. He stated that they were very common in Hong Kong, Japan, and Hawaii.

Additional notes on the distribution of *S. buccaneeri* are given below; occurrences discussed are shown in Figure 1.

S. buccaneeri was first noticed on cruise 116 in the stomach contents of 4- to 12-kg bigeye tuna that were caught from a "boiling" school (see Scott, 1969) at lat 4°N and long 119°W. It was found again the next day in the stomach contents of skipjack tuna caught at lat 5°N on long 119°W, about 700 miles from Clipperton Island, the closest land. This occurrence is of interest because this species previously had been recorded only near land masses.

On cruise 117, *S. buccaneeri* was observed to be a common organism eaten by skipjack and yellowfin tunas, kawakawa, and dolphin caught around the Samoa Islands. Although it was very often eaten by tunas close to shore, it was neither seen nor caught while baiting in the inshore areas. Similarly, Robert E. K. D. Lee (pers. comm.) has found it eaten by yellowfin tuna and kawakawa caught near shore in the Fiji area but has not observed it during baiting operations in inshore waters.

In May of 1971 on cruise 53 of the *Townsend Cromwell*, *S. buccaneeri* juveniles were collected under a night light while the vessel was anchored in a depth of 25 m on Condor Reef in the Caroline Islands.

An estimated 20 kg of *S. buccaneeri* were caught in a close-to-surface haul made with a modified Cobb pelagic trawl (see Higgins, 1970 for a description of this trawl) 160 miles east of Agrihan Island in the Mariana Islands on cruise 55 of the *Cromwell* in November 1971. It was present in five other trawl hauls, in the stomach contents of a wahoo, *Acanthocybium solandri*, caught northwest of Ponape, and in several skipjack tuna caught by trolling north of Namorik during the same cruise.

John Naughton, National Marine Fisheries Service, Honolulu, informed me that several schools of yellowfin and skipjack tunas fished by the Hawaiian fishing vessel *Anela* around Majuro and Arno Atolls in April 1972 were feeding on schools of an anchovy resembling *S. buccaneeri*.

Wilson[3] cited that two Palauans trolling between Angaur and Peleliu Islands observed and sampled a school of kawakawa feeding on *S. buccaneeri*.

The occurrence of *S. buccaneeri* as discussed here in the equatorial eastern Pacific, Samoa Islands, Caroline Islands, Mariana Islands, Palau Islands, Marshall Islands, and Fiji in conjunction with previous records shows it to be a widespread Indo-Pacific (including eastern Pacific) species. Because it occurs in great abundance locally, such as at Fiji and the Samoa Islands, it is to be expected that details of its occurrence will be more likely noted.

SIZE

Most of the anchovies found in the stomach contents were in poor condition. The caudal fin and snout of many specimens were so badly digested that their standard lengths could only be estimated. The *S. buccaneeri* found in the bigeye tuna stomachs ranged from 30 to 57 mm in standard length (SL). Those found eaten by the skipjack tuna ranged from 20 to 58 mm. Those caught on cruise 117 of the *Charles H. Gilbert* near Samoa ranged from 23 to 78 mm. The samples from Condor Reef measured 15 to 30 mm while those from the trawl hauls caught close to the Mariana Islands ranged from 14 to 70 mm. The small postlarvae were semitransparent when alive and turned whitish when preserved in Formalin. They were identified by their exposed urohyal plate and posterior extent of their maxilla.

The presence of large numbers of postlarvae more than 100 miles from land, and adults as far as 700 miles from land, strongly suggests that this species is capable of completing its life cycle in an oceanic environment.

[3] Wilson, P. T. Observations of various tuna bait species and their habitats in the Palau Islands. Unpublished manuscript. Marine Resources Division, Trust Territory of the Pacific Islands, Saipan, Marianas 96950.

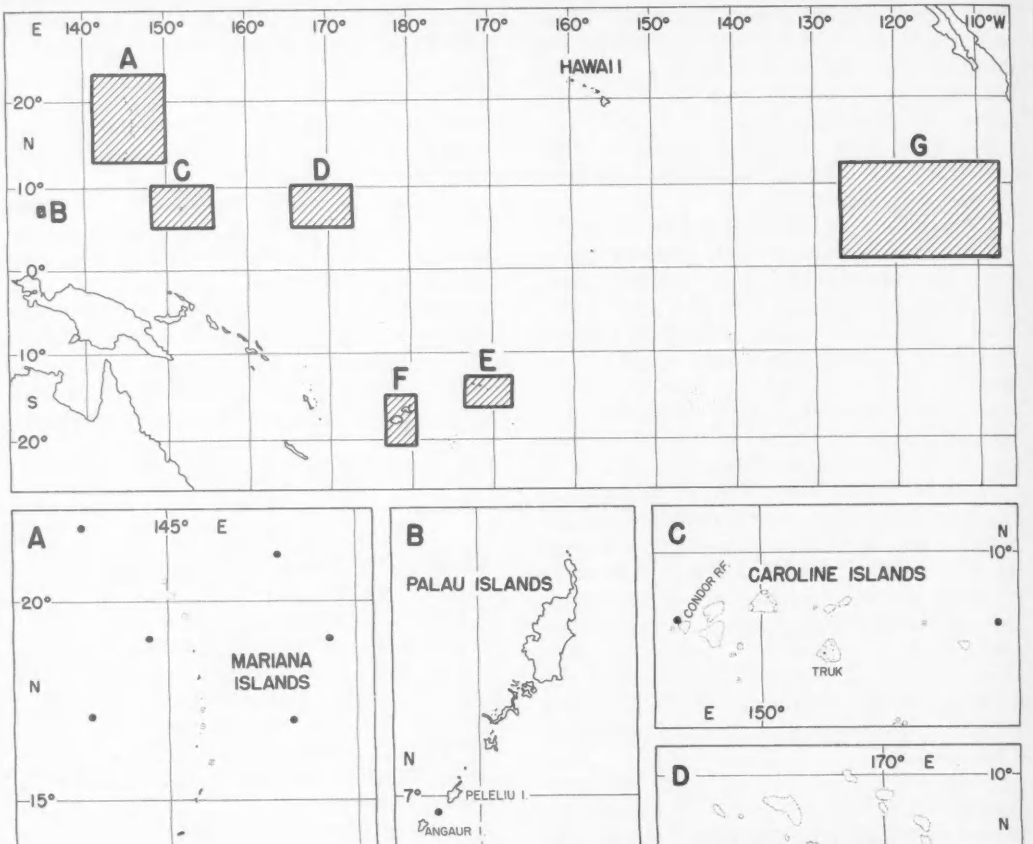

FIGURE 1.—The distribution of *Stolephorus buccaneeri* in the Pacific covered in this study.

FECUNDITY

Ova of 32 specimens of *S. buccaneeri* obtained from tuna stomach contents were measured: Specimens were 38-55 mm SL. From each subsample, diameters of 30 or more of the ova from the most advanced mode were taken. Their distribution ranged from 0.4 to 0.8 mm and peaked at 0.5 mm. The ova were opaque, granulated, and classified as maturing.

Since there are no previous estimates of fecundity, ova from the most advanced mode from two *S. buccaneeri* ovaries were counted. This method was based on the assumption that all of the ova in this mode constituted a single spawning. A 44-mm specimen contained 595 ova in her left ovary and 830 in her right, a total of 1,398. A 39-mm individual had 340 ova in her left ovary and 454 in her right, a total of 794.

FOOD STUDY

The examination of 58 stomach contents of *S. buccaneeri* recovered from tuna stomachs showed that crustaceans were important in their diet, as shown in Table 3. Only one stomach was found empty. The stomachs of *S. buccaneeri* in this study contained primarily calanoid copepods and other organisms. The copepods that were abundant in one or more anchovy stomachs from the equatorial eastern Pacific were *Candacia truncata* and *Euchaeta marina*. The cyclopoid copepod, *Oncaea venusta*, was common in one stomach. Copepods found in abundance in one or more anchovy stomachs taken from tunas caught from the Samoa Islands were *Candacia bispinosa* (?) *C. catula, C. truncata, Centropages gracilis, Euchaeta marina* and *Temora discaudata. C. truncata* and *E. marina* were the only two species that were abundant in both areas. Not unexpectedly, the close-to-shore samples from Samoa were represented by more species than those of the oceanic equatorial eastern Pacific. It should be noted, however, that there were many copepodites and badly digested specimens in the equatorial eastern Pacific samples, while those from the Samoa Islands were larger and in much better condition for identification purposes. Hiatt (1951) examined the stomach contents of the nehu, *S. purpureus*, caught from five major baiting areas in Hawaii and concluded that nehu were selective feeders in that they took the crustacean elements in the plankton. He found important food items to be copepods, ghost shrimp (*Lucifer*), barnacle nauplii, shrimp larvae, and crab larvae.

ACKNOWLEDGMENTS

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TABLE 3.—The stomach contents of *Stolephorus buccaneeri* found in tuna stomachs in the equatorial eastern Pacific and the Samoa Islands (A = abundant, C = common, P = present). [The numbers examined are in parentheses.]

Food items	Samoa Islands			Equatorial eastern Pacific	
	Skipjack tuna (10)	Yellowfin tuna (6)	Kawakawa (4)	Bigeye tuna (23)	Skipjack tuna (15)
Copepoda:					
Calanoids:					
Candacia bispinosa (?)	A	--	--	--	--
Candacia catula	A	P	--	--	--
Candacia simplex	P	--	--	--	--
Candacia truncata	A	--	--	--	A
Candacia sp.	--	--	P	--	--
Centropages gracilis	A	--	--	--	--
Centropages sp.	--	--	P	--	--
Eucalanus sp.	--	--	P	--	--
Euchaeta concinna	P	--	--	--	--
Euchaeta marina	A	--	--	A	--
Euchaeta sp.	--	--	P	P	P
Lucicutia flavicornis	P	--	--	--	--
Nannocalanus minor (?)	--	P	--	--	--
Pleuromamma xiphias	P	--	--	--	--
Scolecithricella ctenopus	P	--	--	--	--
Scolecithrix danae (?)	C	--	--	--	--
Temora discaudata	A	P	--	--	--
Temora sp.	--	--	P	--	--
Undinula darwini	P	--	--	--	--
Unidentified calanoids	P	P	P	C	A
Cyclopoids:					
Copilia mirabilis	P	--	--	--	--
Copilia sp.	--	--	P	--	--
Corycaeus limbatus (?)	--	P	--	--	--
Corycaeus speciosus	P	--	--	P	--
Corycaeus vitreus (?)	P	--	--	--	--
Corycaeus sp.	P	P	--	P	P
Farranula concinna (?)	P	--	--	--	--
Farranula gibbula (?)	P	P	--	--	--
Farranula sp.	--	P	P	P	--
Microsetella rosea	P	P	--	--	--
Microsetella norvegica (?)	--	P	--	--	--
Oncaea conifera	--	--	--	P	--
Oncaea venusta	--	--	--	C	--
Oncaea sp.	P	P	--	P	P
Sapphirina gastrica (?)	P	--	--	--	--
Sapphirina sp.	P	--	P	P	--
Unidentified cyclopoids	--	P	P	A	C
Amphipoda	P	--	--	--	--
Mysidacea	--	--	--	P	--
Shrimp juvenile	C	P	P	P	P
Crab megalops	--	--	P	--	--
Chaetognatha	A	P	P	P	P
Gastropod larvae	P	P	--	--	--
Heteropoda:					
Atlanta inclinata	P	--	--	--	--
Atlanta sp.	P	--	--	--	--
Bivalve larvae	--	P	--	--	--
Ostracoda	P	P	--	--	--
Polychaeta	P	--	--	--	--
Pteropoda:					
Creseis virgula	--	--	--	--	P
Unidentified fish	P	--	P	--	--

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HARVEST AND REGROWTH OF TURTLE GRASS (*THALASSIA TESTUDINUM*) IN TAMPA BAY, FLORIDA[1]

JOHN L. TAYLOR,[2] CARL H. SALOMAN,[3] AND KENNETH W. PREST, JR.[3]

ABSTRACT

A comparison of leaf growth and new leaf production in plots of cut and uncut turtle grass, *Thalassia testudinum*, indicated that plants suffered no damage when harvested twice during a 6-month growing season in Boca Ciega Bay (Tampa Bay), Fla. In deeper or warmer waters where the growing season is protracted, three or more cuttings per year may prove practical.

One of the environmental catastrophes to occur in the past 30 years is the destruction of vast beds of turtle grass through dredge-fill operations, other types of coastal engineering, and pollution in its many forms (McNulty, 1961; Taylor and Saloman, 1968; McNulty, Lindall, and Sykes, in press). The most recent development that may affect turtle grass is the possibility of its harvest for use as a food supplement for livestock.

Interest in the nutrient content of turtle grass was first stimulated by Burkholder, Burkholder, and Rivero (1959), who showed that turtle grass leaves contain about 13% protein. Their analysis was substantiated by Bauersfeld et al. (1969), who further found that turtle grass in pellet form significantly increased the weight gain and feed utilization of experimental sheep over that of control animals when added to normal rations as a replacement for alfalfa at a level of about 10%. One of the many questions raised by the success of these feeding trials is whether or not beds of turtle grass can survive and regrow after harvest. This report presents results of a study in which leaves in an experimental plot of turtle grass were repeatedly cut, measured, and compared with those taken from a control area between August 1968 and November 1969.

In the Gulf of Mexico and Caribbean Sea, the dominant sea grass is turtle grass, *Thalassia testudinum* Koenig and Sims. Generally, it flourishes in estuaries and coastal waters from the level of low water to depths of 10 m or more depending on water clarity. Throughout its range in the central, western Atlantic, turtle grass meadows attain maximum development in muddy sands where average salinity is between 25 and 39‰ (Phillips, 1960; Hartog, 1970). Morphological features of turtle grass have been reported by Tomlinson and Vargo (1966) and Tomlinson (1969a, b), who showed that new grass beds are established from seeds, which mature during spring and summer months, or vegetatively by rhizome fragments that are broken off and relocated by storm action and currents. Kelly, Fuss, and Hall (1971) demonstrated that the normally slow and uncertain spread of turtle grass can be accelerated by transplanting and securing sprigs treated with naphthelene acetic acid. This procedure may prove useful in establishing and replacing turtle grass in unvegetated areas—especially through the northern part of its range where apparently there is little or no seed production (Phillips, 1960).

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Ecologists have shown that the turtle grass community exhibits great biological diversity and forms the basis of an extremely stable and productive ecosystem (Margelef, 1962; Odum, 1967). Its roots and rhizomes penetrate the bottom down to 25 cm or more in a matlike network that effectively binds and holds sediments and detritus against erosion, and provides a unique habitat for many benthic invertebrates (Bernatowicz, 1952; Voss and Voss, 1955; Ginsburg and Lowenstam, 1958; Phillips, 1960; Strawn, 1961; Thomas, Moore, and Work, 1961; O'Gower and Wacasey, 1967; Hartog, 1970). The broad, elongate leaves of turtle grass have a surface area of about 18 m^2 for each square meter of sediment they occupy, and usually represent a standing crop in excess of 1 metric ton (dry weight) per acre (Phillips, 1960; Gessner, 1971). Furthermore, leaves of turtle grass moderate water movements, offer attachment sites for various algae and sessile invertebrates, and serve as a feeding ground, shelter, and nesting area for many fishes and motile invertebrates (Humm, 1964; Stephens, 1966). The rich microbial biota that reduces and recycles much of the organic production from turtle grass beds has been recently described by Fenchel (1970).

PROCEDURE

Turtle grass leaves were harvested in August and October 1968 and in July and September 1969. The cutting was done within a 30 m^2 experimental plot in lower Boca Ciega Bay (Tampa Bay), Fla., where the standing crop of turtle grass on a dry, whole weight basis was 1,198 g/m^2 (Taylor and Saloman, 1968). The harvesting machine was designed and constructed by personnel at the Fisheries Service laboratory in College Park, Md., and consisted of an adjustable, motor-driven sickle bar mounted on a small, styrofoam barge. The cutting head was set about 10 cm above the bay bottom, and the barge was directed by hand as water depth was little more than 1 m at high tide.

Between harvests, weekly samples of at least 100 leaves were picked from plants dug by shovel within the experimental plot and from uncut plants that served as controls in the surrounding area. The point of leaf removal was at the leaf node. Leaf length was measured from both sample sets, and as an additional measurement of plant vigor, the number of new shoots per leaf cluster was also recorded from each set.

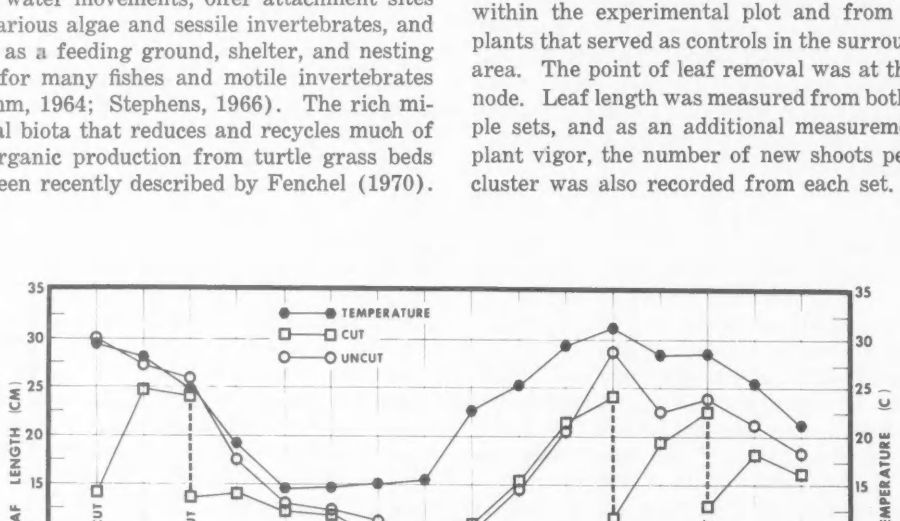

FIGURE 1.—Average monthly length of turtle grass leaves from cut and uncut plants, and related water temperatures in Boca Ciega Bay (Tampa Bay), Fla., between August 1968 and November 1969.

LEAF GROWTH AND REGROWTH AFTER HARVEST

Growth of turtle grass foliage and ultimate leaf length are largely controlled by water temperature and depth (Phillips, 1960; Strawn, 1961). In Tampa Bay, turtle grass normally exhibits a seasonal growth cycle in which leaves elongate rapidly from April to July and die back to short stubble between October and March. During the period of maximum leaf growth, blades develop at a rate of 5 cm per month or more and reach a total length of about 30 cm (Figure 1). Leaves harvested in the growing season had an equivalent or greater rate of regrowth and reached the height of uncut plants in about 2 months (Figure 1). Observed growth rates of both cut and uncut leaves were comparable to figures previously reported from southern Florida by Thomas et al. (1961) and Zieman (1968). Furthermore, harvesting had no apparent influence on production of new leaves. For each month, the average number of shoots produced by both cut and uncut plants was nearly the same (Figure 2).

Thus, from a comparison of leaf growth and new leaf production among cut and uncut plants, it seems likely that turtle grass in the Tampa Bay area can be harvested twice each year without adversely influencing plant vigor.

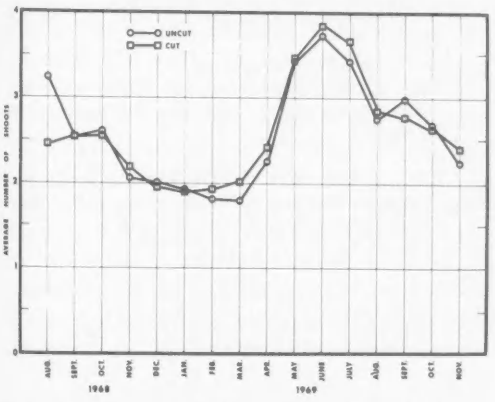

FIGURE 2.—Average monthly number of new shoots per leaf cluster for cut and uncut turtle grass plants sampled in Boca Ciega Bay (Tampa Bay), Fla., between August 1968 and November 1969.

DISCUSSION

Our findings show that turtle grass beds can sustain periodic cutting without apparent damage at intervals of about 2 months in the growing season. In deeper or warmer waters of the Gulf and Caribbean where turtle grass has a longer growing season, it may be practical to harvest leaves more than twice per year. Inherent, technical problems presented by offshore harvesting would probably be offset by the fact that turtle grass in deep water generally has longer leaves and greater biomass than plants growing in shallow areas (Burkholder et al., 1959; Phillips, 1960).

Offshore along the west coast of Florida estimates show that turtle grass grows over about 4 million acres of the sea floor, and in the Caribbean, turtle grass resources are even greater. Thus, the tonnage of turtle grass available for harvest is very large (Bauersfeld et al., 1969). However, from the standpoint of resource management, there are a number of questions that must be resolved before the harvest of turtle grass can be seriously considered by commercial enterprises. Principal queries include: (1) can turtle grass leaves regrow normally after more than two seasons of harvesting; (2) how are other plant and animal members of the turtle grass community influenced by harvesting operations; (3) what would be the consequences of removing vast amounts of primary production from the food webs in coastal waters; (4) would removal of foliage cause serious erosion of sediments in and around turtle grass beds; and (5) how would harvesting methods alter water clarity, and thereby influence populations of phytoplankton and pelagic fishes, and water recreation?

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THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE TOXICITY OF CADMIUM TO THE FIDDLER CRAB, *UCA PUGILATOR*

JAMES O'HARA[1]

ABSTRACT

The concentrations of cadmium lethal to the fiddler crab, *Uca pugilator*, were determined for various environmental regimes of temperature and salinity. Mortality was greatest in high temperatures and low salinities when tested for 240 hr. Concentrations of cadmium were greatest in green gland followed by gill, hepatopancreas, and muscle.

The waste discharge of electroplating plants, lead and zinc mines, and chemical plants frequently contains toxic cadmium salts which contribute to the widespread environmental pollution (McKee and Wolf, 1963), and the importance of this pollutant has been stressed by its relationship with the crippling "itai-itai" disease of Japan (Kobayashi, 1971). The effects of cadmium on aquatic organisms have been investigated for numerous freshwater organisms (Doudoroff and Katz, 1953; Ball, 1967; Mount and Stephan, 1967), and while the cadmium is normally flushed down to the estuarine and marine environments, only Gardner and Yevich (1970), Jackim, Hamlin, and Sonis (1970), and recently Eisler (1971) have examined the effects of cadmium on estuarine forms. Eisler alone has reported the effects of normal variations in salinity and temperature on the toxic effect of cadmium on mummichogs.

The present report is part of a program to examine the effects of chronic exposure of cadmium to fiddler crab, *Uca pugilator*. This study examines the synergistic role of salinity and thermal stress on the acute toxicity of cadmium to the crabs.

METHODS

Fifteen adult male ($\bar{x}$ = 2.2 g) and 10 adult female ($\bar{x}$ = 1.5 g) fiddler crabs were placed in 23 × 30 cm plastic boxes along with 250 ml of dilute filtered seawater. The containers were slightly tilted in the incubator so that the crabs could freely select total or partial immersion. No avoidance of the toxic solution was noted. Desired salinities were obtained by the addition of distilled water. The cadmium stock for all experiments was reagent grade $CdCl_2 \cdot 2\text{-}\frac{1}{2}\ H_2O$ made up to a stock solution of 1 mg Cd^{++} per ml water. Aliquots of this stock were added to each test chamber to bring the cadmium concentration to the desired levels of 1.0, 5.0, 10.0, 25.0, and 35.0 ppm Cd^{++}. All crabs were kept in constant temperature boxes on a 12-hr light-dark photoperiod for the 10-day duration of the experiment. The water was changed every third day to reduce the buildup of metabolic wastes and to keep the concentration of cadmium near the nominal level. Preliminary tests indicated no loss of cadmium from the test medium without organisms. Eisler (1971) showed less than 5% loss from similar concentrations of cadmium in dilute seawater. Dead organisms were removed every 24 hr during the tests.

To determine the synergistic effects of environmental stresses on the toxicity of cadmium, crabs were exposed to the different cadmium

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concentrations in water of 10, 20, and 30‰ salinity maintained at 10°, 20°, or 30°C. Each experimental group had a control maintained in uncontaminated water, but subjected to the salinity and temperature stresses.

Cadmium concentrations in the tissues of crabs exposed to lethal concentrations were determined by use of radioactive cadmium (^{109}Cd) using the following procedure. Fifteen male and 15 female crabs were placed in 300 ml of filtered seawater of 20‰ salinity at 30°C. Each of three test chambers received 2.3 μc ^{109}Cd and an aliquot of stock soultion to bring the cadmium level to 5, 15, or 25 ppm Cd^{++}. These thermosaline regimes and cadmium concentrations were chosen because the acute toxicity tests show that they cause relatively high mortality rates. Four active animals (two males, two females) were sacrificed from each chamber at 0, 12, 24, 36, 48, and 60 hr. The animals were frozen until dissection of the tissues could be accomplished. Four tissues were digested and analyzed: hepatopancreas, gill, green gland, and thoracic muscle. Individual crabs were analyzed; since results from males and females showed no measurable difference, the results were pooled. Concentrations of ^{109}Cd were determined by liquid scintillation on a Packard Tricarb Model 3320 counter.[2] Since each 2.3 μc represented 1.5, 4.5, or 7.5 mg of cadmium in the test water, a simple ratio of counts per minute to microgram of cadmium was determined from spiked samples and used to calculate the amount of cadmium in the tissues. Concentrations of cadmium are expressed as parts per million wet weight of tissue.

RESULTS

ACUTE TOXICITY

In general, the higher temperatures and lower salinities produced the greatest cadmium toxicity. The susceptibility of fiddler crabs to cadmium was most pronounced in the thermosaline regime of 30°C and 10‰. The concentration fatal to 50% of the organisms in 240 hr (TLm-240 hr) was calculated to be 2.9 ppm Cd^{++} (American Public Health Association, 1971). At higher cadmium concentrations, the time required to kill 50% of the crabs was considerably reduced.

TABLE 1.—Cadmium concentrations (Cd^{++} in ppm) lethal to 50% of test organisms (TLm) at different salinities, times, and temperatures.

Salinity	Time	Temperature		
		10°C	20°C	30°C
‰	hr	ppm	ppm	ppm
10	48	--	--	11.0
	96	--	32.2	6.8
	144	51.0	21.3	4.0
	192	28.5	18.0	3.0
	240	15.7	11.8	2.9
20	48	--	--	28.0
	96	--	46.6	10.4
	144	--	23.0	5.2
	192	52.0	16.5	3.7
	240	42.0	9.5	3.5
30	48	--	--	33.3
	96	--	37.0	23.3
	144	--	29.6	7.6
	192	--	21.0	6.5
	240	47.0	17.9	5.7

Table 1 shows the influence of temperature, salinity, and cadmium concentration on the level of toxicant which kills 50% of the crabs in different time periods. The effect of temperature was extremely pronounced and TLm values were generally more influenced by temperature changes than by salinity levels within a thermal regime. The influence of salinity on the TLm-240 hr was most pronounced at 10°C and 10‰ and at higher cadmium concentrations in shorter times. The combined role of temperature and salinity on cadmium toxicity indicates that temperature is less influential at higher salinities.

TISSUE ACCUMULATION

Gills

In the first 12 hr of exposure, gill tissue accumulated cadmium in proportion to the exposure concentration (Figure 1). Thus, gill tissue from crabs exposed to 25 ppm Cd^{++} contained 110 ppm; gill tissue from those exposed

[2] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service, NOAA.

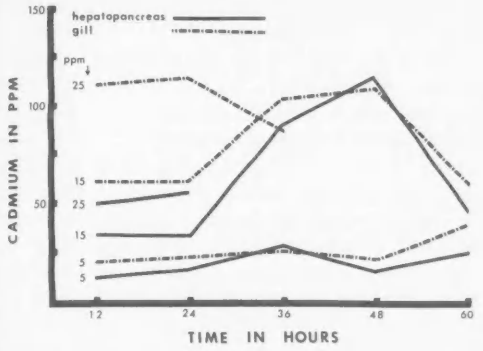

FIGURE 1.—Concentration of cadmium in gill and hepatopancreas of crabs in 5, 15 and 25 ppm Cd^{++} at 30°C, 20‰.

to 15 ppm Cd^{++} contained 59 ppm, while such tissue from those exposed to 5 ppm Cd^{++} contained 18 ppm. Each accumulation in gill tissue was about four times the concentration of cadmium in the surrounding water.

Gill tissues from crabs in 25 ppm Cd^{++} did not increase their cadmium concentration appreciably over 110 ppm in 24 hr and exhibited a decline in tissue concentration at 36 hr. The large mortality rate at 48 hr prevented reliable samples from being obtained. Gill tissue from crabs exposed to 15 ppm Cd^{++} showed an increase in cadmium content between 24 and 48 hr with a maximum accumulation of 109 ppm. The significance of the value around 110 ppm is unclear, but may represent a maximum tissue burden in terms of equilibrium with the external medium. The cadmium concentration in gill tissues from crabs sacrificed at 60 hr showed a marked reduction in cadmium content. Considering the large mortality of crabs in this concentration, the lower cadmium content in the tissues probably represents a reduced binding of the metal due to the destruction of tissue.

Crabs exposed to 5 ppm Cd^{++} continually concentrated cadmium in their gill tissue with a maximum of 39 ppm after 60 hr. No mortality occurred in this concentration, and only one animal died during this period in the acute toxicity tests. Significant mortality occurred only after 96 hr.

Hepatopancreas

The hepatopancreas from crabs in the different cadmium solutions concentrated cadmium about two times exposure level in 12 hr (25 ppm was concentrated to 50 ppm in tissue, 15 to 32 ppm in tissue, and 5 to 11 ppm in tissue). The hepatopancreas tissue in crabs exposed to the highest concentration was almost completely destroyed after 24 hr and precluded samples from these crabs (Figure 1). The hepatopancreas was changed from a firm glandular tissue to an amorphous and liquified condition. Crabs exposed to 15 ppm Cd^{++} showed an increase in cadmium levels to about 116 ppm in 48 hr, followed by a rapid decline. This decline might be associated with the destruction of the hepatopancreas tissue. Crabs exposed to water containing 5 ppm showed the same general increase in Cd^{++} concentration that was evident in gill tissue with a maximum of 24 ppm after 60 hr.

Green Gland

The bioaccumulation was highest in the green gland tissue (Figure 2) with maximum concentrations of 380 ppm in tissue from crabs exposed to 25 ppm, 171 ppm from crabs in 15 ppm, and 118 ppm from crabs in 5 ppm. These values are 12 to 20 times the exposure concentrations.

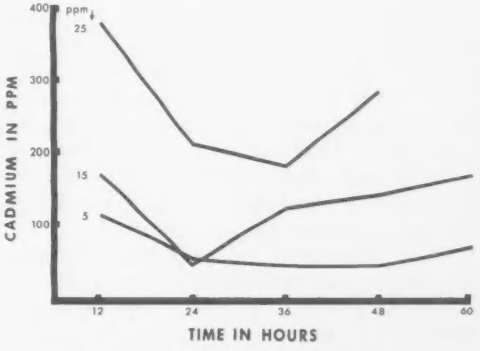

FIGURE 2.—Concentration of cadmium in green gland tissue of crabs in 5, 15 and 25 ppm Cd^{++} at 30°C, 20‰.

At all exposure levels the highest tissue accumulation occurred in the first 12 hr. At 24 hr, the concentrations in the green glands had shown a considerable decline and then increased steadily with values remaining over 10 times the exposure level. The 48-hr determination of 280 ppm is based on only two samples and needs verification.

Muscle

Muscle tissue remained almost constant over the entire time of the experiment, and tissue levels remained only slightly above the exposure levels with maximum concentrations of 29.3 ppm in crabs exposed to 25 ppm, 17.3 ppm from crabs in 15 ppm, and 8.9 ppm from crabs exposed to 5 ppm.

DISCUSSION

Cadmium toxicity is related to both temperature and salinity. The acute toxicity data for crabs maintained at different temperatures show a time delay in the onset of the lethal effect of cadmium. Whether this delay is due to differences in bioaccumulation rates or to differences in a temperature-dependent metabolic response to the metal remains to be examined. Fiddler crabs are often exposed to temperatures well in excess of 30°C, and higher temperatures would further accentuate the toxic effects of small amounts of cadmium.

There is a clear relationship of high susceptibility of fiddler crabs to cadmium in a low-salinity water. It has not been determined if this is due to interaction between the metal and the variety of salts in the seawater resulting in a nontoxic precipitate forming in proportion to the salinity (Bryan, 1971) or if the direction of the osmotic gradient in the higher salinities reduces the rate of entry of the metal.

The rapid accumulation of cadmium from the surrounding water results in considerable tissue destruction in the first 24 hr. High concentrations of cadmium were found in the gills and hepatopancreas of fiddler crabs. Similar results have been reported in crustacea exposed to zinc and mercury (Bryan, 1966; Vernberg and Vernberg, 1972) although high metal concentrations in the green glands were not reported for these metals. Gardner and Yevich (1970) reported gill tissue destruction in the mummichog beginning after 20 hr exposure to cadmium. The data presented here for Cd^{++} concentrations in fiddler crab gills indicate that 24 hr is the time when the cadmium content in crabs exposed to high Cd^{++} concentrations is reduced by tissue destruction. Yager and Harry (1966) showed a decrease in cadmium concentration in the liver of snails exposed to high concentrations of cadmium but attributed this decline to individual variation rather than to tissue destruction.

Mount and Stephan (1967) suggested that there is a threshold concentration of cadmium in the gill tissue of fishes and that death occurs when this concentration is exceeded. This threshold may be around 110 ppm for fiddler crabs.

The relationship between cadmium toxicity and temperature and salinity variation illustrates that physiological stresses, even within the usual ecological range experienced by the animals, lowers the tolerance of organisms to environmental pollutants.

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FISHES, MACROINVERTEBRATES, AND HYDROLOGICAL CONDITIONS OF UPLAND CANALS IN TAMPA BAY, FLORIDA[1]

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ABSTRACT

Faced with statutory restraints that prohibit dredging and filling of estuarine bottoms, coastal developers have turned to alternate methods of providing water front property for homesites. One method, recently used in Tampa Bay, Fla., is the construction of access canals that lead from open water to upland acreage.

This paper presents biological and hydrological data from new upland canals together with some comparative data from older upland canals and bayfill canals. In all types of canals, as presently engineered, stratified, stagnant water causes low levels of dissolved oxygen in summer months, resulting in mortality or emigration among resident organisms. Means of alleviating the problems are discussed.

Among Florida's 322,000 ha of estuarine habitat less than 2 m deep, about 24,000 ha have been filled by coastal developers (Marshall, 1968). Public indignation over indiscriminant and unregulated exploitation of these areas has stimulated legislative action designed to conserve and protect natural resources in estuarine areas that remain (Linton and Cooper, 1971). Faced with statutory restraints, coastal developers have, in some instances, abandoned plans for further bay filling and now seek alternate ways to create premium homesites that will satisfy ever-increasing public demand for waterfront property. One way is the construction of access canals that lead from open water to upland acreage (Barada and Partington, 1972). This method was recently used in Tampa Bay in northeast St. Petersburg, Fla., to connect a housing development with the estuary.

Shortly after draglines removed earth plugs between the excavated canal system and the bay, property owners gave this Laboratory permission to monitor the canals so that ecological conditions in the manmade waterways could be documented. This report contains ecological data recorded at canal and control stations during the first 13 months after the waterway system was completed. Conditions within the upland canal are compared with those recorded in bayfill canals of Boca Ciega Bay, Fla., and older upland canals.

DESCRIPTION OF AREA

The study area, known as Tanglewood Estates, is located at the southern end of Old Tampa Bay on a tract of land that was originally drained by a small tidal inlet of approximately 0.5 ha (Figures 1 and 2). During development, the inlet was dammed and pumped dry. Canals were dug to a depth of approximately 4 m below mean low water and stabilized by concrete seawalls (Figure 3). Bay water was introduced into the ditches in June 1970 creating a canal system of approximately 1.6 ha. Average tidal range in the canal system is about 1 m.

PROCEDURES

Hydrological (five stations) and biological (four stations) samples were collected monthly

[1] Contribution No. 78, Gulf Coastal Fisheries Center, St. Petersburg Beach Laboratory, National Marine Fisheries Service.

[2] Gulf Coastal Fisheries Center, National Marine Fisheries Service, NOAA, 75 33d Avenue, St. Petersburg Beach, FL 33706.

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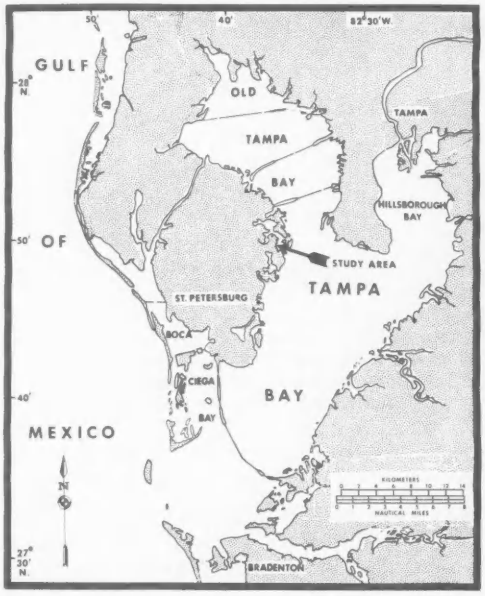

FIGURE 1.—Tampa Bay, Fla., showing location of study area.

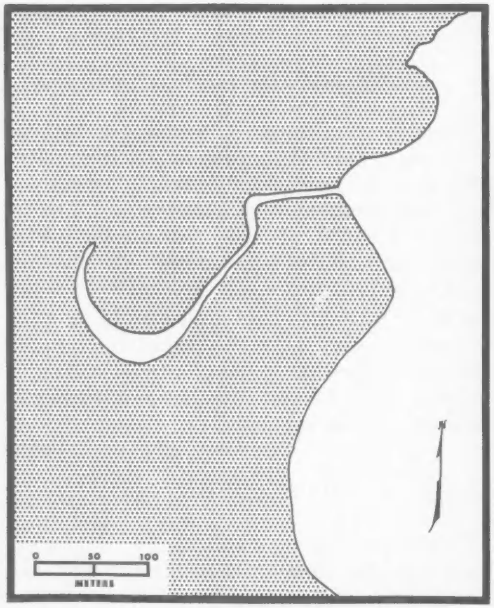

FIGURE 2.—Study area before alteration.

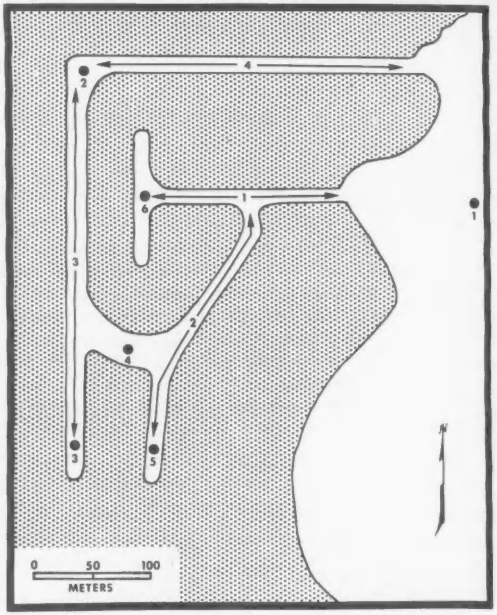

FIGURE 3.—Study area after alteration (hydrologic station ●; trawl station ⟷).

within the canals between 0830 and 1130 hr from August 1970 through August 1971. Also, a hydrological control station, Station 1, was established in the bayou adjacent to the development site to monitor ambient water conditions in a natural area (Figure 3). Hydrological factors were recorded from surface and bottom water and included water temperature, dissolved oxygen, and salinity. Temperature was recorded to the nearest tenth of a degree with a handheld mercury thermometer; dissolved oxygen was determined by a modified Winkler method (Strickland and Parsons, 1968); and salinity was determined with a Model 10401 TS Goldberg refractometer[3].

Fish and invertebrates were collected with a 4.8-m otter trawl composed of a 2.5-cm stretched

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

mesh body fitted with a 0.6-cm mesh inner liner in the cod end. No suitable control station for trawling was established in the adjacent bayou because of numerous snags and oyster beds. Specimens from the trawl were killed in a 10% Formalin-seawater solution and transferred to 50% isopropyl alcohol for preservation. All specimens were identified to species and enumerated.

RESULTS

TEMPERATURE

Only small differences were recorded between surface and bottom water temperature at canal stations or the control station in any sampling period (Table 1). With few exceptions, bottom temperatures were slightly lower than surface temperatures in all months except July and August 1971 when the situation was reversed. The greatest difference observed was at Station 4 in February when bottom temperature was 1.8°C lower than temperature at the surface.

SALINITY

Drought conditions prevailed throughout the Tampa Bay area during most of the study period, and, as a result, salinity rose almost steadily from 23.2‰ in August 1970 to greater than 30.0‰ by July 1971 (Table 1). During this period salinity at the control station was similar to that in the canals. Heavy rains in August 1971 reduced salinity values considerably. This was the only time during the study when stratification occurred at all stations. Bottom salinity at the control station was 9.0‰ higher than

TABLE 1.—Monthly hydrologic measurements of surface and bottom water, August 1970-August 1971.

Stn.	Depth	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Mean
							Temperature (°C)								
1	S	29.8	27.6	24.8	14.8	17.4	14.9	21.0	19.0	26.1	28.0	29.5	28.5	28.5	23.8
	B	--	27.5	24.7	14.7	16.7	14.7	20.8	19.0	26.4	27.8	29.5	29.0	29.4	23.4
2	S	29.5	27.4	24.8	14.8	17.2	15.2	20.8	19.2	25.8	27.8	29.0	29.0	28.4	23.8
	B	--	27.7	25.2	14.5	16.5	14.8	20.2	18.8	25.5	27.4	29.0	30.5	29.5	23.3
3	S	29.0	28.8	25.8	15.7	17.2	15.6	20.6	19.4	25.3	27.8	29.5	29.5	28.4	24.1
	B	--	28.5	24.7	15.5	17.0	15.6	19.7	18.4	25.1	27.2	29.4	30.1	30.0	23.4
4	S	29.5	28.7	25.5	15.2	17.3	16.1	20.6	18.7	25.5	28.0	29.4	29.1	28.5	24.0
	B	--	28.0	24.5	14.2	16.8	15.2	18.8	18.3	25.6	27.0	29.4	29.8	29.8	23.1
5	S	29.5	27.9	25.8	15.8	17.2	15.3	20.9	19.0	25.5	28.0	30.5	29.4	28.8	24.1
	B	--	27.8	24.9	15.3	17.0	15.2	20.7	19.1	25.5	27.0	30.0	30.3	29.8	23.6
6	S	29.5	28.1	25.2	15.5	17.7	16.0	21.0	19.5	25.9	28.2	30.0	29.1	28.8	24.2
	B	--	28.0	25.2	15.3	17.3	15.2	20.8	19.6	25.9	27.4	30.0	29.4	29.3	23.6
							Salinity (‰)								
1	S	24.72	25.67	25.67	27.61	29.00	29.06	26.72	29.78	30.06	29.94	31.39	30.17	13.28	27.16
	B	--	25.56	26.00	27.67	29.11	28.94	26.67	29.83	30.06	29.89	31.28	30.00	22.22	28.10
2	S	23.44	25.00	26.56	28.00	28.78	29.00	27.22	29.72	30.00	29.17	30.06	29.94	13.33	26.94
	B	--	25.28	26.56	27.94	28.72	29.06	27.94	29.67	29.89	29.33	30.72	30.22	27.89	28.60
3	S	23.22	25.11	26.11	27.94	29.00	29.06	27.39	29.44	29.89	29.17	30.61	29.61	13.61	26.94
	B	--	25.28	26.11	27.94	29.00	28.94	27.78	29.56	29.89	29.83	30.39	30.11	28.61	28.62
4	S	23.39	24.89	26.17	28.00	29.06	28.83	27.72	29.06	30.00	29.28	30.33	29.94	13.89	26.97
	B	--	24.56	26.44	27.89	29.06	29.06	27.67	30.06	30.11	29.72	30.83	29.00	28.00	28.62
5	S	23.39	25.11	26.39	28.06	28.94	29.00	27.61	29.44	29.89	29.61	30.72	29.28	13.89	27.03
	B	--	25.44	25.83	28.00	28.94	28.94	27.67	29.72	29.89	29.17	30.72	30.06	26.78	28.43
6	S	25.22	24.67	26.39	27.94	29.11	29.06	27.28	29.17	29.94	29.44	30.28	28.67	14.06	27.01
	B	--	24.56	26.28	27.94	28.89	28.83	27.50	29.83	29.89	29.83	30.44	29.00	25.72	28.23
							Dissolved oxygen (ml/liter)								
1	S	3.87	3.06	3.46	5.80	4.67	5.64	4.35	4.75	4.03	3.06	2.90	2.58	2.34	3.86
	B	--	3.62	3.38	5.64	4.83	5.23	4.35	4.67	4.11	2.98	3.06	2.66	2.18	3.89
2	S	4.19	3.87	4.43	5.72	4.43	5.07	4.67	4.91	3.22	4.27	3.14	2.18	3.63	4.13
	B	--	3.78	4.03	5.15	3.95	4.75	2.49	4.19	1.37	3.95	3.14	1.86	0.89	3.30
3	S	4.35	2.98	4.03	5.47	4.99	5.07	4.91	3.95	2.74	3.95	4.35	3.14	4.03	4.15
	B	--	2.66	2.42	5.40	4.51	4.35	1.13	3.10	1.62	2.98	3.46	0.00	0.82	2.70
4	S	4.35	2.26	4.27	5.64	4.75	5.31	4.67	3.78	2.66	4.59	3.62	3.30	4.67	4.14
	B	--	2.02	2.42	4.67	3.70	4.59	0.57	3.46	2.22	2.00	2.50	0.66	0.65	2.46
5	S	3.62	3.06	4.43	5.40	4.85	5.72	3.95	4.27	2.50	3.87	3.87	3.54	4.99	4.16
	B	--	2.90	4.35	5.23	4.75	4.59	2.66	3.14	2.34	2.98	3.81	0.08	0.57	3.12
6	S	4.19	2.90	4.51	5.64	5.15	5.23	4.75	4.67	3.30	3.22	3.71	2.98	4.43	4.12
	B	--	2.82	4.35	5.55	5.14	4.75	4.59	4.27	2.42	3.14	3.38	2.50	0.17	3.59

the surface. The stratification was even more evident at canal stations where the difference between surface and bottom values ranged between 11.6‰ (Station 6) and 15.0‰ (Station 3). In general, the most landward stations exhibited the greatest differences between surface and bottom salinities.

OXYGEN

Daytime concentrations of dissolved oxygen at the surface and bottom for each station are shown in Table 1. Only at the control station were surface and bottom values similar, varying linity at the control station was 9.0‰ higher than no more than 0.6 ml/liter at any one sampling time throughout the year. At this station the lowest observed concentration was 2.1 ml/liter (August 1971). Surface oxygen values within the canal system were comparable with those at the control station throughout the year. However, bottom oxygen dropped in the canals in February when less than 2.0 ml/liter was recorded at Stations 3 and 4. These values rose above 3.0 ml/liter in March, but in April and May dissolved oxygen near 2.0 ml/liter or less was recorded at several canal stations. In July less than 1.0 ml/liter was recorded at Stations 3, 4, and 5, and by August less than 1.0 ml/liter of oxygen was recorded at the bottom at all canal stations.

To determine the diel changes in oxygen concentration during the July sampling period, a 24-hr sampling program was conducted at each station. Results showed that surface and bottom values were similar only at the control station (Figure 4). Surface oxygen concentration in the canals corresponded with values recorded at the control station and never fell below 2.0 ml/liter. However, at all canal stations the bottom was nearly anoxic throughout the 24-hr sampling period.

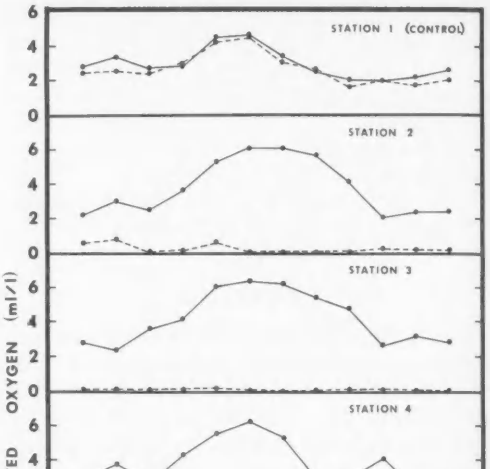

FIGURE 4.—Results of 24-hr oxygen survey in July 1971 (surface · ——— · ; bottom · - - - - - - - - ·).

FISHES AND MACROINVERTEBRATES

Thirty-six species and 10,497 individuals of vertebrates and invertebrates were collected within the canals during the year (Table 2). Of the 36 species, 32 were finfish (23 of sport or commercial value), 1 was the diamondback terrapin, *Malaclemys terrapin*, and 3 were commercially important invertebrates (blue crab, *Callinectes sapidus;* pink shrimp, *Penaeus duorarum;* and brief squid, *Lolliguncula brevis*).

The four species of fish caught in greatest abundance represented 92% of the total number of specimens. They were the bay anchovy (*Anchoa mitchilli*), spotfin mojarra (*Eucinostomus argenteus*), spot (*Leiostomus xanthurus*), and silver jenny (*Eucinostomus gula*). The bay anchovy alone made up nearly 72% of the total.

The brief squid was by far the most abundant invertebrate (84% of all invertebrates collected)

TABLE 2.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at all stations from August 1970 through August 1971. No individual collected in July and August 1971.

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
												Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:													
Anchoa mitchilli[1]	56	539	1,582	26	0	93	698	1,375	746	16	2,425	7,557	72.0
Eucinostomus argenteus[1,2]	0	120	135	241	220	153	16	25	6	0	5	921	8.8
Leiostomus xanthurus[1,2]	0	1	0	0	26	24	108	661	1	0	0	821	7.8
Eucinostomus gula[1,2]	0	0	18	82	164	99	1	8	0	0	0	372	3.5
Micropogon undulatus[1,2]	0	0	0	0	0	0	1	20	7	34	9	71	0.7
Cynoscion arenarius[1,2]	0	0	0	3	10	8	20	8	0	0	2	51	0.5
Menticirrhus americanus[1,2]	0	0	3	15	13	1	1	0	1	4	5	43	0.4
Pogonias cromis[1,2]	0	0	1	0	3	7	4	4	4	0	1	24	0.2
Archosargus probatocephalus[1,2]	0	0	0	2	10	4	2	1	1	2	1	23	0.2
Lagodon rhomboides[1,2]	0	0	1	4	6	3	0	6	1	0	0	21	0.2
Microgobius gulosus[2]	0	0	0	0	0	0	1	11	2	0	0	14	0.1
Cynoscion nebulosus[1,2]	0	3	4	4	0	0	1	0	0	0	2	14	0.1
Chaetodipterus faber[1]	0	0	4	0	1	2	0	1	1	0	4	13	0.1
Arius felis[1,2]	0	0	0	0	1	0	3	5	3	0	0	12	0.1
Malaclemys terrapin	0	0	0	2	0	0	0	1	5	4	0	12	0.1
Bairdiella chrysura[1,2]	0	0	1	0	2	5	1	0	0	0	1	10	0.1
Gobiosoma bosci[2]	0	0	0	0	0	0	0	7	1	1	0	9	0.1
Prionotus tribulus[2]	0	1	1	4	1	0	0	0	0	0	0	7	0.1
Orthopristis chrysoptera[1,2]	0	0	1	0	0	0	0	2	3	0	1	7	0.1
Sphoeroides nephelus[1]	0	0	0	3	1	1	0	0	0	0	0	5	0.1
Opisthonema oglinum[1]	0	0	0	0	0	0	0	0	0	0	4	4	0.0
Dasyatis sabina[2]	0	0	1	0	0	0	2	0	0	0	0	3	0.0
Mugil cephalus[1,2]	0	0	0	0	0	1	1	0	0	0	0	2	0.0
Chloroscombrus chrysurus[1]	0	0	0	0	0	0	0	0	0	2	0	2	0.0
Anchoa hepsetus[1]	0	0	0	0	0	0	0	0	0	0	2	2	0.0
Achirus lineatus[2]	0	0	0	0	0	0	0	0	0	0	2	2	0.0
Synodus foetens[1,2]	0	0	0	0	1	0	0	0	0	0	0	1	0.0
Opsanus beta[2]	0	0	0	0	0	0	0	1	0	0	0	1	0.0
Symphurus plagiusa[2]	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Sciaenops ocellata[1,2]	0	0	0	0	1	0	0	0	0	0	0	1	0.0
Paralichthys albigutta[1,2]	0	0	0	1	0	0	0	0	0	0	0	1	0.0
Chasmodes saburrae[2]	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Gymnura micrura[2]	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Invertebrates:													
Callinectes sapidus[1,2]	0	8	2	2	1	5	3	9	12	4	1	47	0.5
Penaeus duorarum[1,2]	0	4	2	7	2	4	5	1	0	0	1	26	0.3
Lolliguncula brevis[1]	0	45	55	93	43	4	15	6	29	87	20	395	3.8
Total species	1	8	15	15	18	19	18	19	16	9	17	36	
Total individuals	56	721	1,811	489	506	417	883	2,153	821	154	2,485	10,497	100.0

[1] Of commercial or sport value.
[2] Demersal or bottom feeder.

and made up nearly 4% of the total number of animals collected during the year.

The first trawl sample was made in August 1970, 2 months after bay water was introduced in the canal system. At that time the only species of fish found in the canals was the bay anchovy, and 98% of the specimens were taken at Station 4 (Figure 3; Tables 3, 4, 5, 6). By September, the blue crab, pink shrimp, brief squid, and four additional species of finfish were caught within the canal system. Station 4 contained seven species of vertebrates and invertebrates while Stations 2 and 3 contained five species each. No specimens were yet found at Station 1.

In October, 5 months after water was introduced, fishes and invertebrates were found in all canals, and a total of 15 species were collected. Station 4, with 11 species, still contained the greatest faunal diversity. Stations 1, 2, and 3 contained 10, 5, and 4 species, respectively.

Through the winter, spring, and early summer months (November through June) an average of 16 species per month was collected throughout the area. The number of species and individuals at each station declined in April and May corresponding to reduction in dissolved oxygen, but in June the number of species and individuals increased again at all stations.

TABLE 3.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station I from August 1970 through August 1971. No individual collected in August and September 1970 and in July and August 1971.

Species	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
										Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:											
Anchoa mitchilli	118	16	0	1	77	31	0	9	412	664	58.9
Eucinostomus argenteus	49	1	6	51	13	9	5	0	4	138	12.3
Leiostomus xanthurus	0	0	2	3	41	50	0	0	0	96	8.5
Eucinostomus gula	10	3	41	39	0	0	0	0	0	93	8.3
Micropogon undulatus	0	0	0	0	0	1	0	21	0	22	2.0
Menticirrhus americanus	1	0	4	0	0	0	1	0	0	6	0.5
Archosargus probatocephalus	0	1	2	0	1	0	1	0	0	5	0.4
Malaclemys terrapin	0	2	0	0	0	1	0	2	0	5	0.4
Cynoscion arenarius	0	1	0	1	0	0	0	0	2	4	0.4
Lagodon rhomboides	0	0	0	2	0	1	1	0	0	4	0.4
Opisthonema oglinum	0	0	0	0	0	0	0	0	4	4	0.4
Microgobius gulosus	0	0	0	0	0	2	2	0	0	4	0.4
Chaetodipterus faber	1	0	0	0	0	0	1	0	1	3	0.3
Prionotus tribulus	1	2	0	0	0	0	0	0	0	3	0.3
Cynoscion nebulosus	0	2	0	0	0	0	0	0	0	2	0.2
Pogonias cromis	0	0	0	0	0	0	0	2	0	2	0.2
Orthopristis chrysoptera	1	0	0	0	0	0	0	0	1	2	0.2
Sphoeroides nephelus	0	2	0	0	0	0	0	0	0	2	0.2
Bairdiella chrysura	0	0	0	1	0	0	0	0	0	1	0.1
Chloroscombrus chrysurus	0	0	0	0	0	0	0	1	0	1	0.1
Gobiosoma bosci	0	0	0	0	0	1	0	0	0	1	0.1
Invertebrates:											
Lolliguncula brevis	5	3	6	1	4	0	0	16	5	40	3.6
Callinectes sapidus	1	0	0	2	3	1	7	3	1	18	1.6
Penaeus duorarum	2	1	0	1	2	0	0	0	0	6	0.5
Total species	10	10	6	9	8	9	8	7	8	24	
Total individuals	189	134	61	101	142	97	20	52	430	1,126	100.0

In the latter part of June, after our monthly sample, a severe outbreak of red tide occurred in a large part of Tampa Bay, including the study area. Massive fish kills were noted in the Bay through most of July (Karen Steidinger, Florida Department of Natural Resources Biological Laboratory, pers. comm.). Data are not available on the size of the kill, but an estimated 3,000 tons of various species were removed from beaches in the Bay area (Lloyd Dove, St. Petersburg Public Works Director, pers. comm.). No live specimens were collected in the study area during July or August. The absence of specimens during this period corresponded with low dissolved oxygen at the bottom.

DISCUSSION

At least 36 of the 265 species of finfish, shrimp, and crabs known to inhabit the Tampa Bay area (Springer and Woodburn, 1960; Dragovich and Kelly, 1964; Sykes and Finucane, 1966) utilized the study area throughout most of the year. It was not surprising to find bay anchovy as the dominant species as it is known to be dominant in bayfill canals of Boca Ciega Bay, Fla., (Taylor and Saloman, 1968) and in housing development canals in Texas (unpublished data[4]).

Although the majority of individual fishes taken in the study area was plankton feeders, most of the species (26) were demersal or bottom feeders based on knowledge of their life histories (Darnell, 1958; Springer and Woodburn, 1960; Odum, 1971). Taylor and Saloman (1968), using the same trawl size and procedures as in our study, reported that no demersal fishes were taken in bayfill canals of Boca Ciega Bay. However, examination of additional, unpublished data[5] from canals in Boca Ciega Bay showed that

[4] Unpublished data on file at Gulf Coastal Fisheries Center, National Marine Fisheries Service, NOAA, Fort Crockett, Building 302, Galveston, TX 77550.

[5] Unpublished data on file at Gulf Coastal Fisheries Center, National Marine Fisheries Service, NOAA, 75 33d Avenue, St. Petersburg, FL 33706.

TABLE 4.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station 2 from August 1970 through August 1971. No individual collected in August 1970 and in July and August 1971.

Species	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
											Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:												
Anchoa mitchilli	23	800	8	0	21	384	1,083	480	2	1,392	4,193	86.0
Leiostomus xanthurus	0	0	0	5	1	0	4	0	0	0	353	7.2
Eucinostomus argenteus	13	46	0	29	40	3	5	1	0	0	137	2.8
Eucinostomus gula	0	5	1	22	15	1	0	0	0	0	44	0.9
Micropogon undulatus	0	0	0	0	0	0	4	0	8	1	13	0.3
Lagodon rhomboides	0	0	0	5	1	0	4	0	0	0	10	0.2
Menticirrhus americanus	0	0	0	3	0	0	0	0	4	2	9	0.2
Cynoscion arenarius	0	0	0	1	0	3	3	0	0	0	7	0.1
Gobiosoma bosci	0	0	0	0	0	0	4	1	1	0	6	0.1
Bairdiella chrysura	0	0	0	0	4	0	0	0	0	1	5	0.1
Arius felis	0	0	0	0	0	0	3	1	0	0	4	0.1
Malaclemys terrapin	0	0	0	0	0	0	0	3	1	0	4	0.1
Cynoscion nebulosus	2	0	0	0	0	0	0	0	0	1	3	0.1
Sphoeroides nephelus	0	0	1	1	1	0	0	0	0	0	3	0.1
Microgobius gulosus	0	0	0	0	0	0	3	0	0	0	3	0.1
Archosargus probatocephalus	0	0	0	2	0	0	0	0	0	0	2	0.0
Chaetodipterus faber	0	0	0	0	0	0	0	0	0	2	2	0.0
Pogonias cromis	0	0	0	0	1	0	0	0	0	1	2	0.0
Anchoa hepsetus	0	0	0	0	0	0	0	0	0	0	2	0.0
Gymnura micrura	0	0	0	0	1	0	0	0	0	0	1	0.0
Prionotus tribulus	0	0	1	0	0	0	0	0	0	0	1	0.0
Synodus foetens	0	0	0	1	0	0	0	0	0	0	1	0.0
Chasmodes saburrae	0	0	0	0	1	0	0	0	0	0	1	0.0
Opsanus beta	0	0	0	0	0	0	1	0	0	0	1	0.0
Dasyatis sabina	0	1	0	0	0	0	0	0	0	0	1	0.0
Invertebrates:												
Lolliguncula brevis	2	15	0	2	0	0	2	18	13	4	56	1.2
Callinectes sapidus	4	0	2	1	0	0	1	2	0	0	10	0.2
Penaeus duorarum	0	0	3	1	0	0	0	0	0	1	5	0.1
Total species	5	5	6	12	10	5	12	8	6	10	28	
Total individuals	44	867	16	92	92	426	1,399	507	29	1,407	4,879	100.0

at least 13 of 21 species of fishes collected by trawl may be considered bottom feeders. Based on these data, it appears that new upland canals provide a better habitat for fishes than do much older bayfill canals in the sense that the former support greater abundance of species and individuals.

Undoubtedly, the lack of fish in the canals of Tanglewood Estates during the last 2 months of the study was due in part to effects of the red tide. Decomposition of the dead fish increased oxygen demand on the system during this period, but decline in dissolved oxygen in April and May and corresponding decline in the number of species and individuals indicated the system was deteriorating prior to the red tide outbreak. Our continued study will determine to what degree the system is stressed by low summer oxygen in the absence of red tide.

Others working in the Tampa Bay system have reported low bottom oxygen in areas of poor water circulation and soft sediment. Dragovich, Kelly, and Finucane (1966) recorded less than 2 ml/liter in June and August from a dredged location in central Boca Ciega Bay. In dredged and undredged areas of Hillsborough Bay, reduced oxygen near the bottom is common during the summer. There, the lack of dissolved oxygen has been attributed to sludge deposited from sewage, as well as high water temperature and poor water circulation (Saloman, Finucane, and Kelly, 1964; U.S. Federal Water Pollution Control Administration, Southeast Region, 1969). A similar condition is shared by older upland canals throughout south Florida (Barada and Partington, 1972) and certain housing development canals in Texas (see footnote 4). Oxygen depletion in all of these areas is the result of poor

TABLE 5.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station 3 from August 1970 through August 1971. No individual collected in July and August 1971.

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
												Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:													
Anchoa mitchilli	1	337	39	1	0	19	29	43	266	2	506	1,243	53.8
Eucinostomus argenteus	0	26	11	145	144	41	0	11	0	0	0	378	16.4
Leiostomus xanthurus	0	0	0	0	0	7	14	310	0	0	0	331	14.3
Eucinostomus gula	0	0	0	36	84	19	0	8	0	0	0	147	6.4
Cynoscion arenarius	0	0	0	2	9	6	0	5	0	0	0	22	1.0
Micropogon undulatus	0	0	0	0	0	0	0	5	5	3	4	17	0.7
Menticirrhus americanus	0	0	0	7	6	1	0	0	0	0	0	14	0.6
Pogonias cromis	0	0	0	0	1	2	4	3	1	0	0	11	0.5
Archosargus probatocephalus	0	0	0	0	2	2	1	1	0	0	0	6	0.3
Chaetodipterus faber	0	0	1	0	1	2	0	1	0	0	1	6	0.3
Arius felis	0	0	0	0	0	0	1	1	2	0	0	4	0.2
Cynoscion nebulosus	0	0	0	2	0	0	1	0	0	0	0	3	0.1
Microgobius gulosus	0	0	0	0	0	0	0	3	0	0	0	3	0.1
Lagodon rhomboides	0	0	0	1	0	0	0	1	0	0	0	2	0.1
Mugil cephalus	0	0	0	0	0	1	1	0	0	0	0	2	0.1
Achirus lineatus	0	0	0	0	0	0	0	0	0	0	2	2	0.1
Gobiosoma bosci	0	0	0	0	0	0	0	2	0	0	0	2	0.1
Malaclemys terrapin	0	0	0	0	0	0	0	0	2	0	0	2	0.1
Bairdiella chrysura	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Chloroscombrus chrysurus	0	0	0	0	0	0	0	0	0	1	0	1	0.0
Dasyatis sabina	0	0	0	0	0	0	1	0	0	0	0	1	0.0
Orthopristis chrysoptera	0	0	0	0	0	0	0	0	1	0	0	1	0.0
Prionotus tribulus	0	1	0	0	0	0	0	0	0	0	0	1	0.0
Symphurus plagiusa	0	0	0	0	0	1	0	0	0	0	0	1	0.0
Invertebrates:													
Lolliguncula brevis	0	15	4	65	2	2	1	4	0	1	4	98	4.2
Callinectes sapidus	0	2	0	0	0	0	0	5	0	1	0	8	0.4
Penaeus duorarum	0	0	0	1	1	0	1	1	0	0	0	4	0.2
Total species	1	5	4	9	9	13	10	16	6	5	5	27	
Total individuals	1	381	55	260	250	104	54	404	277	8	517	2,311	100.0

circulation, accumulation of soft, organically rich sediments, and storm-water runoff from residential and agricultural areas.

Developers in the Tampa Bay area could reduce these problems in future projects through better design of canal systems. This would involve: (1) elimination of dead-end canals and (2) limiting depths to the euphotic zone approximately 1.5 m (5 ft) below mean low water. A flow-through system without deadends would insure better tidal exchange and circulation. Also, by limiting depths to approximately 1.5 m below mean low water, the canals probably would not serve as silt traps as readily as deeper canals, and stratification of the water column would be eliminated. In addition, light penetration would occur throughout the water column thereby allowing oxygen production through photosynthesis by benthic algae and diatoms.

Elimination of dead-end canals and limiting depths to the photic zone will not necessarily insure adequate flushing, however. A major factor that must be taken into account is water exchange through tidal action. Tidal range in most of Florida is very small, varying from 0.3 m to about 1.0 m, and will provide adequate water exchange in canals only short distances from the shoreline. Our data show serious oxygen depletion in the deep, dead-end canals only 150 m inland of the shoreline (Station 6). A safe distance for shallower, flow-through canals can best be determined by an environmental engineer knowledgeable of the tidal range and circulation patterns adjacent to the upland to be developed.

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TABLE 6.—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at Station 4 from August 1970 through August 1971. No individual collected in July and August 1971.

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total	
												Number	Percent
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*		
Vertebrates:													
Anchoa mitchilli	55	179	625	1	0	52	208	219	0	3	115	1,457	66.8
Eucinostamus argenteus	0	81	29	95	41	21	0	0	0	0	1	268	12.3
Eucinostomus gula	0	0	3	42	17	26	0	0	0	0	0	88	4.0
Leiostomus xanthurus	0	1	0	0	0	7	18	15	0	0	0	41	1.9
Micropogon undulatus	0	0	0	0	0	0	1	10	2	2	4	19	0.9
Cynoscion arenarius	0	0	0	0	0	1	17	0	0	0	0	18	0.8
Menticirrhus americanus	0	0	2	8	0	0	1	0	0	0	3	14	0.6
Archosargus probatocephalus	0	0	0	1	4	2	0	0	0	2	1	10	0.5
Pogonias cromis	0	0	1	0	2	4	0	1	1	0	0	8	0.4
Cynoscion nebulosus	0	1	4	0	0	0	0	0	0	0	1	6	0.3
Lagodon rhomboides	0	0	1	3	1	0	0	0	0	0	0	5	0.2
Arius felis	0	0	0	0	1	0	2	1	0	0	0	4	0.2
Microgobius gulosus	0	0	0	0	0	0	1	3	0	0	0	4	0.2
Orthopristis chrysoptera	0	0	0	0	0	0	0	2	2	0	0	4	0.2
Bairdiella chrysura	0	0	1	0	2	0	0	0	0	0	0	3	0.1
Chaetodipterus faber	0	0	2	0	0	0	0	0	0	0	0	2	0.1
Prionotus tribulus	0	0	0	1	1	0	0	0	0	0	0	2	0.1
Sciaenops ocellata	0	0	0	0	1	0	0	0	0	0	0	1	0.1
Paralichthys albigutta	0	0	0	1	0	0	0	0	0	0	0	1	0.1
Dasyatis sabina	0	0	0	0	0	0	1	0	0	0	0	1	0.1
Malaclemys terrapin	0	0	0	0	0	0	0	0	0	1	0	1	0.1
Invertebrates:													
Lolliguncula brevis	0	28	31	25	33	1	10	0	9	57	7	201	9.2
Callinectes sapidus	0	2	1	0	0	3	0	2	3	0	0	11	0.5
Penaeus duorarum	0	4	0	2	0	3	2	0	0	0	0	11	0.5
Total species	1	7	11	10	10	10	10	8	5	5	7	24	
Total individuals	55	296	700	179	103	120	263	251	17	64	132	2,180	100.0

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MATURITY, SEX RATIO, AND SIZE COMPOSITION OF THE NATURAL POPULATION OF AMERICAN LOBSTER, *HOMARUS AMERICANUS*, ALONG THE MAINE COAST[1]

JAY S. KROUSE[2]

ABSTRACT

From 1968 through 1970, American lobsters, *Homarus americanus*, were collected in coastal water near Boothbay Harbor, Maine. Length-frequency histograms graphically displayed the marked effects of high commercial exploitation on the natural lobster population. Sex ratios approximated a 1:1 relationship for sublegal lobsters (Maine minimum size is 81-mm carapace length). Length-weight relationship was determined for 454 lobsters. Shedding was observed to begin in spring and then peak in late summer.

On the basis of ovarian classification, presence of spermatophores in seminal receptacles, length-frequency distribution of berried females, and morphometric measurements, nearly all females above 100-mm carapace length were assumed to be mature, whereas only a few females between 81- to 90-mm carapace length were mature. Examination of male gonads suggested that male lobsters began maturing at relatively small sizes (50% mature at about 44-mm carapace length).

The American lobster, *Homarus americanus* Milne Edwards, is one of the most valuable and heavily exploited commercial species occurring along the Maine coast. Recognizing the urgent need for biological management of this inshore fishery, the Maine Department of Sea and Shore Fisheries initiated the Lobster Research Program in April 1966. The two primary phases of this program have encompassed: 1) probability sampling of the commercial lobster fishery along the entire Maine coast and 2) collection of prerecruit and legal-sized lobsters (minimum size in Maine is now 81-mm carapace length) near Boothbay Harbor, Maine (this phase began in March 1968). With data from these two independent sampling schemes, various population parameters have been calculated and then ultimately employed to estimate the minimum size limit for maximum sustainable yield (Thomas, 1971).[3]

The objectives of this paper, which are based upon data collections of the natural lobster population from Boothbay Harbor, are concerned with: 1) sex ratios; 2) incidence of molting; 3) length-weight relationship; 4) size composition of catch; and 5) the size at first sexual maturity for both sexes.

METHODS AND MATERIALS

Lobsters were collected in coastal waters near Boothbay Harbor, Maine, from April 1968 through December 1970. The following types of gear were used: (1) rectangular vinyl-coated lobster traps (1- × 2-inch and 1- × 1-inch mesh); (2) elliptical polyethylene lobster traps; (3) conventional wooden lobster traps; (4) a

[1] This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-14-R.

[2] Maine Department of Sea and Shore Fisheries, West Boothbay Harbor, ME 04575.

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shrimp try trawl with a cod end of 1-inch stretch mesh; and (5) a variable mesh monofilament gill net (four 25-ft sections of 1-, 2-, 3-, and 4-inch mesh). SCUBA divers were also employed on a few occasions to collect small male lobsters from which supplemental data were obtained for our maturity studies.

Of the aforementioned types of gear, considerably more fishing effort has been expended with wire traps. This disproportion of effort resulted from early fishing success experienced with wire traps and their relative suitability for hauling from a 17-ft Boston Whaler.[4] Subsequently, only 67 (2.6%) of 2,582 lobsters were captured with the other types of gear.

Carapace length (distance measured along midline from posterodorsal edge of carapace to posterior margin of eye socket) and total length (distance measured dorsally from tip of rostrum to tip of telson) were determined to the nearest millimeter for all lobsters sampled. Wet weights were recorded to the nearest 10 g.

MATURITY STUDY—GONAD EXAMINATION

Males

The vas deferens and/or testes of 204 male lobsters (carapace lengths ranged from 36 to 95 mm) were examined for the presence or absence of spermatophores (Figures 1 and 2). Males having spermatophores were considered mature. Because it was economically objectionable to sacrifice large numbers of lobsters, a method whereby the internal sex organs could be probed or extracted without any detrimental effects to the lobster was desirable. Initially, I attempted to withdraw sperm samples through a blunt hypodermic needle inserted into the vas deferens via its valvular orifice on the fifth pair of pereiopods. This technique produced inconsistent results and had to be abandoned. I then discovered that both the vas deferens and testis could be extracted with a forceps introduced through a small incision at the base of the fifth pair of walking legs. This procedure yielded reliable results and had no noticeable deleterious effects upon lobster survival throughout a postoperative period of several months.

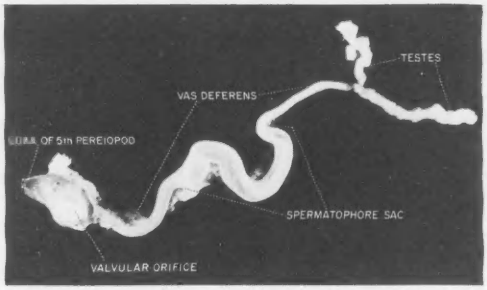

FIGURE 1.—Reproductive system dissected from a male lobster.

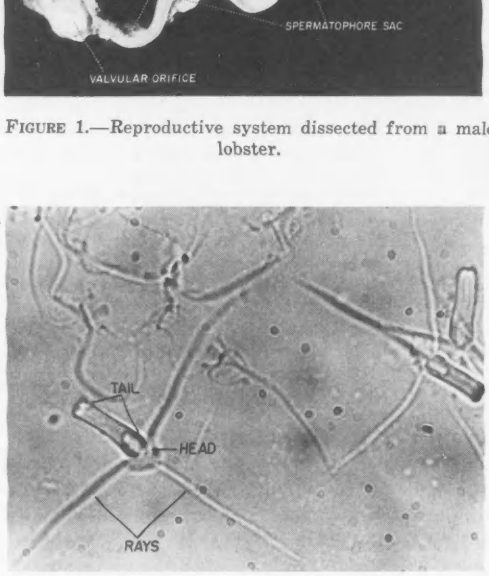

FIGURE 2.—Lobster sperm cells photographed under oil immersion at 970×.

Females

Ovaries were dissected from 158 female lobsters and then ovarian color and ova diameter (to nearest 0.1 mm) were recorded. Egg diameters were based on the average of a random sample of 10 eggs (distorted eggs were rejected) from each ovary. Using the criteria of ovarian color and ova diameter, ovaries were assigned to one of the following stages of development:

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Stage of development	*Ovary color*	*Egg diameter (mm)*
immature	translucent white	$\leqslant$ 0.4
developing	yellow-orange	0.5-0.7
mature	dark green	$\geqslant$ 0.8

Two additional determinations were made for each female: 1) width of the second abdominal segment (distance between deepest part of pleura on ventral surface) and 2) examination of the seminal receptacle (structure where sperm is stored upon copulation until egg extrusion) for the presence of sperm. As a check on my technique for detecting spermatophores, I examined 31 berried lobsters from Canada and found sperm in all of them.

In conjunction with the annual berried female program, during which the State of Maine purchases from the pound owners lobsters that have become ovigerous while in captivity, carapace lengths were recorded for 1,150 berried females.[5] These data were obtained during the period 1966 through 1970.

RESULTS AND DISCUSSION

SEX RATIOS

Sex ratios were analyzed by assigning lobsters from catches during the period 1968 through 1970 to 5-mm carapace length size groups by sex. Midpoints of each size increment were then plotted against the number of lobsters in each of the respective size groups (Figure 3). Although differences did exist between the proportion of males to females within various size classes, these differences were not consistent from year to year, suggesting that they may have been artifacts of sampling. In 1969 and 1970 when the catches were relatively large (greater than 1,000 lobsters), the overall percentages of females were 48.1 and 50.3, respectively. While the sex ratio approached 1:1 in 1969 and 1970, in 1968, when the sample size was half that of the other two years, the proportion of females was 56.4%. This disparity may best be attributed to the smaller sample size in 1968.

[5] Maine law prohibits the possession or sale of egg-bearing female lobsters.

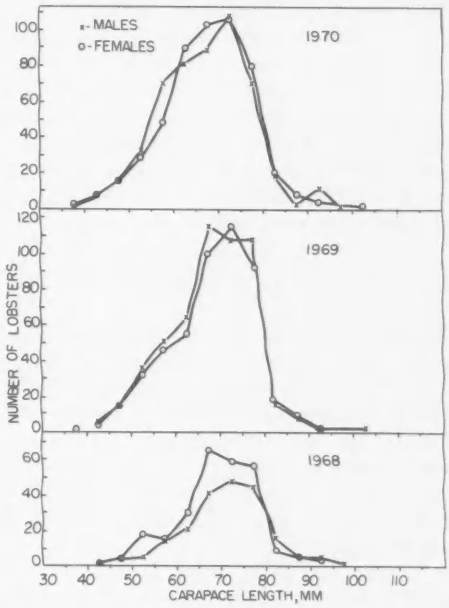

FIGURE 3.—Number of male and female lobsters grouped by 5-mm size classes from Boothbay Harbor, 1968 through 1970.

As the samples were predominantly composed of sublegal lobsters, our estimate of approximately a 1:1 sex ratio suggests that immature female and mature male lobsters have similar molting frequencies and increments of growth. In contrast to this, Herrick (1911), Templeman (1939), and Wilder (1953) have demonstrated that most sexually mature males molt annually and mature females every other year. In a tagging study conducted off Monhegan Island, Maine, Cooper (1970) found no significant differences in growth increments of male and female lobsters (average carapace length of 90 mm). Unlike the Maine findings, studies by Wilder (1963) in Egmont Bay, Prince Edward Island, and Squires (1970) and Ennis (1972) off Newfoundland revealed larger increments of growth for males than females for sizes above about 65-mm carapace length. Based on the maturity work of Templeman (1944), female lobsters from the aforementioned Canadian

study areas attain maturity at smaller sizes (50% mature between 70- to 80-mm carapace length) than Maine females as indicated by results of this present study; thus, I believe this explains why Canadian lobsters exhibited a differential growth rate between sexes, while Maine lobsters (our samples were markedly deficient of mature females) appeared to grow at the same rate regardless of sex.

MOLTING

Lobsters were classified as shedders (recently molted) when their carapace and/or chelipeds were soft to the touch (lacked normal rigidity). Because molting was observed to be concurrent for males and females, shedding data were combined for sexes (Table 1). While a few lobsters were observed to molt in spring, shedding did not reach a peak until September in 1968 and August in 1969 and 1970.

TABLE 1.—Percentage of soft-shelled lobsters in monthly samples from Boothbay Harbor, 1968 through 1970.

Month	1968	1969	1970
January	--[1]	0	--[1]
February	--[1]	--[1]	0
March	--[1]	0	0
April	0	0	4
May	0	0	1
June	0	3	4
July	2	6	19
August	1	10	24
September	16	1	18
October	10	0	17
November	1	--[1]	7
December	0	0	0

[1] No sample collected.

LENGTH-WEIGHT RELATIONSHIP

The regression of total wet weight on carapace length was calculated for 454 lobsters (206 males and 248 females) collected from April 1968 through March 1969. The equation used was $W = aL^b$, where W = wet weight in grams, L = carapace length in millimeters, and a and b are constants. The regression was fitted by the method of least squares using the logarithmic transformation $\log_{10}W = \log_{10}a + b \log_{10}L$.

Analysis of covariance on the regression coefficients as described by Steel and Torrie (1960) revealed no significant difference between sexes, so data from all lobsters were combined. The calculated regression equation was $\log W = -2.9052 + 2.9013 \log L$. This mathematical relationship is represented by the curve in Figure 4.

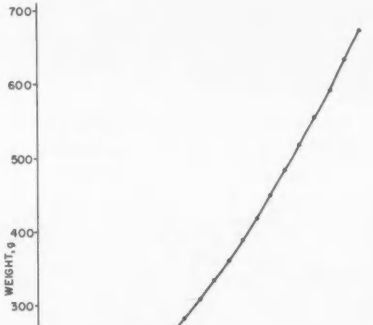

FIGURE 4.—Calculated length-weight relationship for 454 lobsters from Boothbay Harbor. The regression equation is $\log W = -2.9052 + 2.9013 \log L$.

SIZE COMPOSITION OF CATCH

I compiled length-frequency histograms of lobsters collected with wire traps in 1968, 1969, and 1970 (Figure 5). The effects of availability (term encompassing both vulnerability and accessibility) and the high rate of exploitation by the commercial fishery on our annual catches are manifested by the histograms.

The stepwise increase in numbers of lobsters with size up to approximately 70-mm carapace length led me to assume that this mode represented the size at which lobsters were fully vulnerable to our gear. Reduced vulnerability of lobsters smaller than 70-mm carapace length in our samples might best be attributed to the effects of gear selectivity and, possibly, the more seclusive behavior of small lobsters. In ecological studies of the lobster being conducted

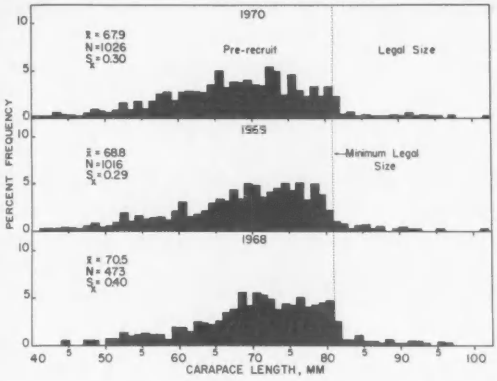

FIGURE 5.—Annual length-frequency distributions of lobsters sampled near Boothbay Harbor, 1968 through 1970.

in the Boothbay Harbor area, SCUBA divers have observed lobsters of less than 40-mm carapace length to be virtually inactive during nocturnal periods and apparently passing most of their early life within subterranean burrows (Richard A. Cooper, pers. comm.).

Sharp reductions in the number of lobsters above the minimum legal size (81-mm carapace length) reflected the influence of commercial exploitation. The legal-sized lobsters composed only 6 to 9% by number of the three annual catches.

For each annual length-frequency distribution, I attempted to select, on an objective basis, modes representative of assumed age or molt groups by analyzing the polymodal frequency distributions graphically with probability paper (Harding, 1949). Unfortunately, I discovered that I could not pick meaningful age or molt group modes due primarily to the limited size range (70- to 80-mm carapace length) over which our samples were considered to be representative of the natural lobster population. Since the increment of a lobster's growth was assumed to be about a 13 to 14% increase in carapace length (Wilder, 1953), it became apparent that our representative size range of 70- to 80-mm carapace length contained, at best, only one mode or possibly more if an age class experienced differential growth.

SIZE AT MATURITY

Males

In the Boothbay Harbor area, 50% of the male lobsters sampled were sexually mature at about 44-mm carapace length (Figure 6). The smallest mature male was 41-mm carapace length. Although sample size was limited for lobsters smaller than 45-mm carapace length, I do not believe that this significantly affected our conclusions.

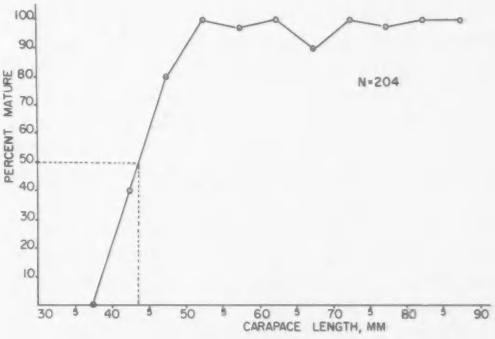

FIGURE 6.—Percentage frequency of mature male lobsters by 5-mm size classes.

In this study, maturity was solely based upon the criterion of presence or absence of sperm cells. Therefore, even though a lobster might appear to be physically mature (possessed sperm cells), this particular individual might be incapable of successfully copulating with a female. In mating experiments, Templeman (1934) observed that male lobsters were unable to mate with considerably larger females. In fact, the success of mating was greatest when the males were slightly larger than the females. As most females in the Boothbay Harbor area mature above the minimum legal size of 81-mm carapace length (discussed in following section), it appears that prerecruit males seldom contribute reproductively to the natural population.

Females

Size-frequency polygons of the three ovarian stages of development indicated that immature ovaries occurred in females from 51- to 89-mm carapace length; developing ovaries in females from 69- to 94-mm carapace length; and mature ovaries in females from 77- to 100-mm carapace length (Figure 7). Although the size ranges of the various ovarian stages overlapped considerably, the following trends are apparent: 1) immature ovaries predominated in females with carapace lengths less than 75 mm; 2) developing ovaries were most common at intermediate sizes (75- to 90-mm carapace length); and 3) mature ovaries gradually increased in frequency at sizes greater than 85-mm carapace length. Unfortunately, owing to difficulty in procuring legal-sized lobsters, the sample size of individuals between 85 and 100 mm in carapace length was limited to 47 lobsters; thus the task of determining size where approximately half the female lobsters became mature was confounded. However, the data indicated that a few females matured between 80- and 90-mm carapace length, but the onset of maturity for most females was at carapace lengths greater than 90 mm. This conclusion is further substantiated and expanded by the following facets of the maturity investigation.

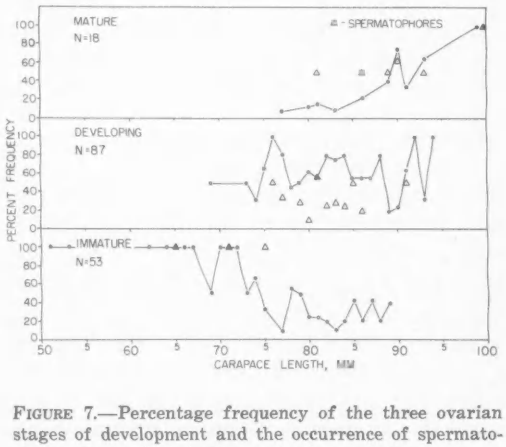

FIGURE 7.—Percentage frequency of the three ovarian stages of development and the occurrence of spermatophores (triangles) in the seminal receptacles.

FIGURE 8.—Number of female lobsters with spermatophores in their seminal receptacles.

Spermatophores, the presence of which was another criterion for maturity, were detected more frequently in the seminal receptacles of mature females, particularly those females larger than 90 mm carapace length (Figures 7 and 8). Only 2 females with carapace lengths less than 75 mm had sperm cells, whereas 7 of 18 (39%) lobsters larger than 89-mm carapace length had spermatophores. From mating experiments, Templeman (1932, 1934) concluded that females had to be soft-shelled for mating to be accomplished successfully. Thus, females without spermatophores, even though their ovaries were classified as mature or well developed, would not be capable of spawning until they had undergone at least another molt and then, while soft-shelled, had copulated with a male. The absence of spermatophores in many females, which were observed to have developing or mature ovaries, suggested that these lobsters would not spawn until they advanced to the next molt class. Thus only 5 of 84 (6%) females from 80- to 90-mm carapace length were considered to be fully mature (possessed mature ovaries along with spermatophores), whereas the remaining 79 lobsters would not spawn until they attained carapace lengths of about 91 to 102 mm (assuming a 14% growth increment).

Templeman (1944) related the onset of sexual maturity of Canadian female lobsters with the relative increase in width of the second abdominal segment to total length. This morpho-

metric relationship was based on Templeman's (1935) observation that the female's abdomen markedly increases in width during maturation. I applied Templeman's method to my data on 482 females from inshore Boothbay Harbor (1968-71) and 31 berried Canadian lobsters (1970) as well as data on 217 females from inshore Boothbay Harbor collected in 1966 by Herbert C. Perkins of the National Marine Fisheries Service, West Boothbay Harbor, Maine. Carapace lengths were grouped by 5-mm size groups, and then abdominal widths of each size group were averaged. Ratios of abdominal width to carapace length were plotted against carapace length, and resulting curves were fitted by eye (Figure 9). Inflection points, which indicated size where maturity began, occurred at approximately 80-mm carapace length for both sets of Boothbay Harbor data. For the offshore population of American lobsters, Skud and Perkins (1969) reported an inflection point of 77 mm. Asymptotes, which denoted the size where all lobsters were assumed to be mature, appeared at about 115 mm for Perkins' Boothbay Harbor data, while an asymptote was not reached for my Boothbay Harbor data. I believe the asymptote at 115 mm was probably deceptively higher

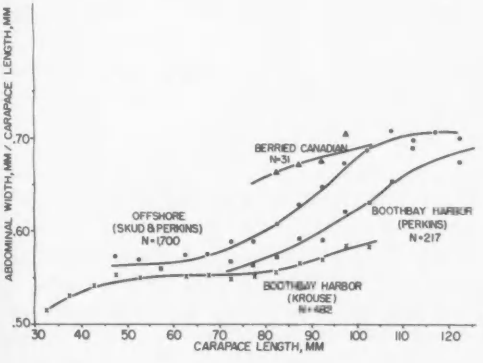

FIGURE 9.—Ratio of abdominal width to carapace length plotted against carapace length for Boothbay Harbor female data collected by Krouse and Perkins, berried Canadian female data, and Skud's and Perkins' study, 1969.

because of an insufficient number of lobsters sampled for sizes above 105 mm, which constituted less than 5% of the total sample. This conclusion was maintained both by Skud's and Perkins' (1969) data that demonstrated an asymptote at 100 mm and by the following section on length frequencies of ovigerous females from Maine. The relatively early maturity of Canadian females, particularly those inhabiting warm water of the southern part of the Gulf of St. Lawrence (Templeman, 1944), is demonstrated in Figure 9.

The length-frequency distribution of berried females taken along the Maine coast (Figure 10) disclosed that a few females began extruding

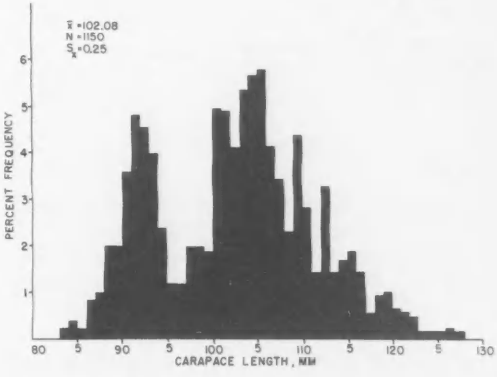

FIGURE 10.—Length-frequency distribution of native Maine berried females, 1966 through 1970.

eggs at 83-mm carapace length while the percentage of ovigerous females gradually increased to the first peak at 91 mm. The most pronounced mode occurred at about 105 mm, which was considered to be the size when nearly all females were mature. It should be mentioned that the modes at 91 and 105 mm corresponded with assumed age or molt class modes determined by Thomas (1971, see footnote 3) from commercial catch data.

The length-frequency distribution of berried females becomes particularly meaningful when compared with percent frequencies of female

lobsters from the commercial catch in the following size classes:

Carapace length	Percentage of total catch: Commercial	Berried females
81-90 mm	80	11
91-100 mm	17	29
>100 mm	3	60

Because lobsters ranging in carapace length from 81 to 90 mm constituted approximately 80% of the commercial catch and only 11% of the berried female sample, it is apparent that only a very small percentage of females mature below 90-mm carapace length. Certainly the most marked disparity in size composition was for carapace lengths greater than 100 mm (3% commercial and 60% berried females). This would seem to validate the previous conclusion that most females above 100-mm carapace length are mature.

SUMMARY

This study which is concerned with the analyses of data collected from 1968 through 1970 on the natural population of American lobsters along the Maine coast has yielded the following information:

1. Sex ratio was 1:1, thus suggesting that differences in growth rate and molting frequency do not exist between mature males and immature females.

2. Molting was concurrent for males and females, with shedding reaching a peak in late summer.

3. The length-weight relationship for sexes combined was $\log W = -2.9052 + 2.9013 \log L$.

4. Length-frequency histograms revealed the high rate of exploitation by the commercial fishery and an increase in unavailability of lobsters progressively smaller than 70-mm carapace length.

5. Male lobsters begin maturing at relatively small sizes (50% mature at about 44-mm carapace length); however, because native Maine females rarely mature below the minimum legal size of 81-mm carapace length and males must approximate females' size to successfully mate, it is doubtful that prerecruit males contribute reproductively to the natural population.

6. Female maturity was assessed by the following methods: 1) classification of ovaries by color and ovum diameter to three stages of development; 2) examination of seminal receptacles for spermatophores; 3) morphometric relationship of abdominal width:carapace length ratio to carapace length; and 4) length-frequency distribution of native Maine berried females. From estimates by these four independent methods, I concluded that females seldom become sexually mature at a size less than 81-mm carapace length, and then only a small fraction of those females between 81 and 90 mm attain maturity, whereas, at carapace lengths greater than 100 mm, nearly all females are assumed to be mature. Bearing in mind the minimum legal size regulation of 81-mm carapace length, I demonstrated in this study that the majority of females are harvested commercially prior to their first opportunity to spawn. An obvious change in management suggested by the results of this study would be to increase the minimum size limit to insure successful spawning by a sizeable portion of the population. Based on results of this study and those from the commercial sampling phase of the Maine lobsters project, Thomas (1971, see footnote 3) deals specifically with minimum size limit increases as a means to achieve a maximum sustainable yield.

ACKNOWLEDGMENTS

I am indebted to James C. Thomas for his guidance and support throughout the course of this study and his review of the manuscript. Richard Hanley, Gerald Brackett, Robert Nunan, Stephen Ham, and Andrew Dolloff assisted with field collections and data compilations. Gareth Coffin of the Northeast Fisheries Center, National Marine Fisheries Service, West Boothbay Harbor, Maine, performed the photographic work.

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APPARENT GROWTH OF YELLOWFIN TUNA FROM THE EASTERN ATLANTIC OCEAN

J. C. LE GUEN[1,2] AND GARY T. SAKAGAWA[1,3]

ABSTRACT

Apparent growth of yellowfin tuna from the eastern Atlantic Ocean was estimated from modal progression of length-frequency distributions by two methods. One was to use fish of unknown age, which gave estimates of parameters of the von Bertalanffy growth function of $L_\infty = 194.8$ cm and $K = 0.035$, on a monthly basis. The other was to use fish of apparent known age, which resulted in $L_\infty = 175.2$ cm and $K = 0.044$. Although the parameter estimates were different, estimates of length at ages 1.5-4.5 years were quite similar with both approaches.

A comparison of growth estimates of yellowfin tuna was made. Estimates from analysis of length-frequency distributions appeared to be superior to those from analysis of scales because they were based on a larger range of fish sizes. However, observed lengths at ages 1.5-5 years were similar for both types of analysis and for yellowfin tuna from both the Atlantic and Pacific Oceans.

It is recommended that observed sizes at age rather than the estimated sizes at age from the von Bertalanffy function be used in estimating yield per recruitment of yellowfin tuna.

There have been several studies (e.g., Le Guen, Baudin-Laurencin, and Champagnat, 1969; Yang, Nose, and Hiyama, 1969) on growth of Atlantic yellowfin tuna (*Thunnus albacares*) but little agreement among them. The disagreement can be traced to at least three sources: first, the kinds of data, e.g., length-frequency distributions and scale readings have been different; second, the method of fitting the von Bertalanffy growth function has varied; and third, the range of fish sizes employed has been different. Because an accurate estimate of growth is important for estimating yield per recruitment by the Beverton and Holt approach (Schaefer and Beverton, 1963), one method that can provide information for rational management of the resource, a study was initiated to estimate growth from the best series of data available and, hopefully, to resolve the disagreement. In this report the results of that study on apparent growth of yellowfin tuna from modal progression of length-frequency distributions are presented and compared to growth estimates derived from published data and computed by standardized procedures.

PLAN OF ANALYSIS

Length frequency samples from commercial landings were employed in our study (Table 1). The fish were caught off Africa by baitboats and purse seiners and were sampled by French and Inter-American Tropical Tuna Commission (IATTC) scientists. (Scientists of the IATTC sampled the Atlantic tuna catch of U.S. vessels under a contract from the National Marine Fisheries Service.) The French scientists sampled the French catches, which were from three general regions—Abidjan, Ivory Coast; Dakar, Senegal; and Pointe-Noire, Congo—and the IATTC scientists sampled the American catches, which were from primarily the Gulf of Guinea. The IATTC samples were caught in both the Abidjan and Pointe-Noire regions, but because

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[3] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

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TABLE 1.—Sources of length data of Atlantic yellowfin tuna caught in the surface fishery off Africa.

Region	Year	Type of length measurement	Type of vessel sampled			Source
			Bait-boat	Small seiner[1]	Large seiner[2]	
Abidjan	1966	Predorsal		X		O.R.S.T.O.M., 1971
	1966-69	Predorsal	X	X		O.R.S.T.O.M., 1971
	1970	Predorsal	X	X	X	O.R.S.T.O.M., 1971
Dakar	1968	Fork	X			Champagnat and Lhomme, 1970
	1969	Predorsal	X	X		Champagnat and Lhomme, 1970
	1970	Predorsal	X	X	X	O.R.S.T.O.M., 1971
Gulf of Guinea	1968-70	Fork			X	Staff, Tuna Population Dynamics Project, 1971[3]
Pointe-Noire	1965-66	Predorsal	X	X		O.R.S.T.O.M., 1971
	1967-68	Predorsal	X	X		Le Guen et al., 1969
	1969	Predorsal	X	X		O.R.S.T.O.M., 1971
	1970	Predorsal	X	X		O.R.S.T.O.M., 1971
	1971	Predorsal	X	X		Unpublished data (Le Guen)

[1] Small purse seiner = less than 500 metric tons capacity.
[2] Large purse seiner = larger than 500 metric tons capacity.
[3] Staff, Tuna Population Dynamics Project. 1971. Size composition of the yellowfin and skipjack tuna purse seine fishery off the west coast of Africa 1968-1970. Unpublished manuscript, 28 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

they could not be separated as such, they were treated separately from the French data.

Two methods were employed in our analysis. One approach ("age unknown") was based on all samples from the four regions, for years 1965-70 and with age of size groups unknown. The second approach ("apparent age known") was slightly different. Only fish that were caught in an area from São Tomé to southern Angola, 1967-71, and with the apparent age of each size group known, were employed.

Growth was estimated with the von Bertalanffy growth function. This function is often expressed as,

$$L_t = L_\infty\ [1 - \exp - K\ (t - t_0)],$$

where L_t = length at age t, L_∞ = asymptotic length, K = growth rate, and t_0 = theoretical age when $L_t = 0$. It is fitted to growth data by various procedures (e.g., Walford, 1946; Abramson, 1963; Ricklefs, 1967; Gulland, 1969; Knight, 1969), most of them require data on size at known age. A least-squares procedure that does not contain this limitation was described by Fabens (1965). He fitted a von Bertalanffy function of the form

$$L_{t+\Delta} = L_t + (L_\infty - L_t)\ (1 - \exp - K)$$

to tag-return data, but his procedure is equally applicable to length observations of untagged fish made at t and again at a later date, $t + \Delta$, when the age of the fish is unknown. For tuna, Rothschild (1967) and Joseph and Calkins (1969) employed Fabens' procedure to estimate growth of skipjack tuna (*Katsuwonus pelamis*) from tagging data. We used the Fabens' procedure with monthly mean lengths for individual year classes to estimate growth of yellowfin tuna of unknown age. A computer program written by Tomlinson (Abramson, 1971) was employed to estimate L_∞ in centimeters and K, expressed on a monthly basis. For growth estimates based on apparent known age fish, we used a computer program written by Abramson (1963) and modified by Psaropulos (1966) of a least-squares procedure described by Tomlinson and Abramson (1961).

ANALYSIS WITH UNKNOWN AGE FISH

METHODS

Fish landed at Abidjan, Dakar, and Pointe-Noire (Figure 1) were measured for predorsal length (tip of snout to anterior base of the dorsal fin) by French scientists; fish were measured for fork length by IATTC scientists. In order to standardize the length measurements, we em-

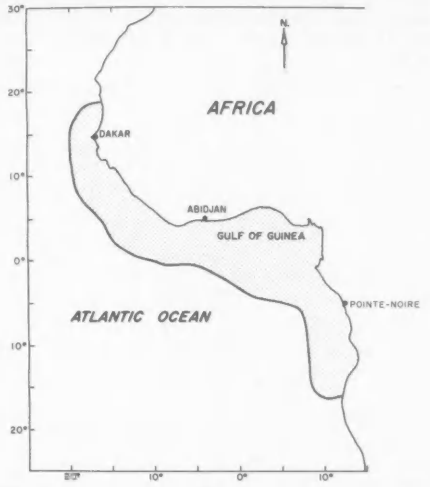

FIGURE 1.—Area off Africa where the surface fishery for yellowfin tuna operates.

ployed the relation, $\log L_f = 0.273 + 1.175 \log L_d$ to convert samples with predorsal length in centimeters (L_d) to fork length in centimeters (L_f). This relation is based on 508 observations and differs from $L_f = (3.624 + 0.212\ L_d)^2$, which was employed by Poinsard (1969). It has a slightly better correlation coefficient ($r = 0.9943$) than Poinsard's equation ($r = 0.9940$) (Lenarz, 1971).[4] Calculated fork lengths based on either equation are accurate only to 1-4 cm.

Monthly length-frequency distributions were tabulated by 4-cm-fork-length groups for samples from each region. Modes were identified and assumed to represent age classes within which lengths were normally distributed. Normal distributions were then fitted to the length frequencies of samples in which two or more modes were present, and the mean length of each age class was estimated (Table 2). A computer program for separating size classes in a mixture that was written and described by Hasselblad (1966) and modified by Tomlinson (1970)[5] was used to separate the age classes and estimate the mean lengths. For samples with only one prominent mode, the modal length, or midpoint of length interval of maximum frequency was considered the "mean length." Representative length-frequency distributions are shown in Figure 2.

Mean lengths for each sample are plotted in Figures 3-6. For each region a serial succession of increasing mean lengths with time was designated a year class, with only one recruited per year although two groups appear to be recruited

[4] Lenarz, W. H. 1971. Length-weight relations for five Atlantic scombrids. Unpublished manuscript, 9 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

[5] Tomlinson, P. K. 1970. Program for separating mixture of normal distributions. Unpublished manuscript, 2 p. California Department of Fish and Game, Operations Research Branch, Long Beach, CA 90802.

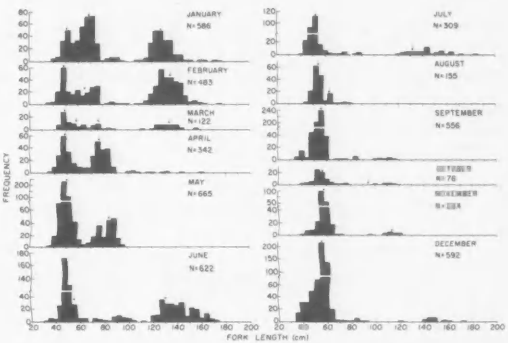

FIGURE 2.—Length-frequency distributions of samples from Pointe-Noire, 1970. Arrows indicate mean lengths of modal groups that were identified by curve fitting.

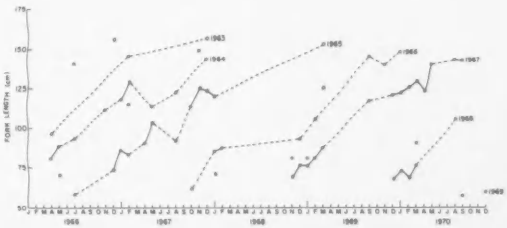

FIGURE 3.—Mean length of size groups of yellowfin tuna as a function of sampling date at Abidjan. Growth of the 1963-69 year classes are indicated

TABLE 2.—Mean lengths (cm) of modal groups identified in samples from Abidjan, Dakar, Gulf of Guinea, and Pointe-Noire. Values that were not used in the analysis of growth are shown in parentheses.

Region	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Abidjan	1966				80.7	(56.8)		59.2				112.0	73.5
					97.2	(70.8)		94.2					(155.2)
						89.4		(140.9)					
	1967	87.3	84.3		92.0	(48.5)			92.8	(56.0)	62.9	65.3	124.6
		118.2	(115.4)			103.8			122.9		114.8	125.3	144.5
			129.7			114.9						149.7	156.8
			146.6										
	1968	(71.7)	88.0									69.4	76.3
		86.2										82.3	94.8
		121.9											
	1969	76.2	81.9	87.9						118.2		140.0	(50.1)
		(82.3)	105.4	112.2						145.6			67.9
				(125.5)									122.4
				153.6									
	1970	(54.8)	69.5	76.9	124.0	140.0			(55.6)	58.1		(48.0)	(43.1)
		73.8	125.3	(92.1)					105.6	143.0		(58.4)	60.6
		123.0		129.4					143.7				
		148.4											
Dakar	1968	(44.0)	(56.3)	(61.2)	(63.5)	72.0	(55.3)	76.0	(63.0)	(58.4)	62.3	66.9	64.0
			117.9	122.3	120.7		70.1		81.2	88.4	89.6	100.1	
							(118.6)						
	1969	(70.1)	75.3	75.5	79.9	(43.6)	(49.0)	(49.1)	(64.8)	(69.4)	62.4	53.2	(61.9)
		79.4	102.6	105.0	113.9	(57.4)	(60.1)	90.9	95.7	102.5	(75.7)	(78.5)	74.0
		102.3				85.4	93.7	107.8	108.2	118.5	123.8	124.5	119.9
						112.2							
	1970	64.8	(49.6)	(49.4)	(51.4)	(50.6)	(53.4)	(55.3)	(56.3)	(39.7)	(42.9)	(30.9)	(46.4)
		124.8	71.8	73.5	72.5	76.2	(70.5)	(72.3)	(74.3)	(56.4)	59.2	(45.0)	(57.4)
			(88.9)	(101.7)	(106.0)	132.4			90.6	92.4	(72.3)	63.0	69.9
			126.0	124.3	126.4				133.7		100.8	108.8	
				145.1	147.2						145.2	146.3	
Gulf of Guinea	1968								62.9	57.8	70.0		
									136.0	77.0	84.4		
									(160.2)	135.8			
	1969								56.8	(52.6)	(59.4)	156.0	
									112.7	120.3	121.5		
									124.7	132.6	153.4		
										151.3			
	1970						(54.8)	(55.5)	(56.0)	66.8	65.6		
							87.1	82.6		140.6	(103.9)		
							141.2	(106.8)					
								143.3					
								165.7					
Pointe-Noire	1965							(57.7)	(57.4)	59.1	60.3	60.0	
								(78.1)	(80.2)	104.0	(78.4)		
								113.0	116.4		121.1		
	1966									(64.0)		63.0	
										99.1		102.2	
										145.3			
	1967			(50.5)		(52.9)	(58.0)	(53.4)	(53.6)	(59.3)	(61.4)	112.0	(68.0)
				86.9		90.6	88.8	102.1	104.0	105.1	108.4		
						113.8			113.0				
						155.9							
	1968	(60.7)				(68.0)	(56.4)	59.7	62.2	64.6	65.9	(75.0)	72.7
		122.7					(73.4)	(71.1)	(73.6)	(75.3)	(76.2)		(89.5)
		(154.6)					120.9	(85.4)	(90.9)	(87.0)	(91.9)		(101.5)
								134.0	130.8	143.8	136.8		
								140.0	152.7	(156.6)			
	1969	76.0		86.3	49.6	100.0	(56.9)	(55.7)	(45.8)	(57.7)	(57.4)	59.9	56.6
				(111.1)	94.3		104.2	(112.9)	(56.3)	112.7	114.6	(127.7)	127.1
					(117.7)			154.5	(117.5)				
					148.4				156.0				
					164.8								
	1970	(51.5)	(48.5)	(48.8)	(48.9)	(49.9)	(50.7)	(51.3)	(53.7)	(56.0)	(55.3)	(57.6)	(56.0)
		69.0	65.5	(57.5)	76.8	82.8	131.8	132.2	62.2		93.5	113.5	
		129.7	134.7	75.6									
				134.1									

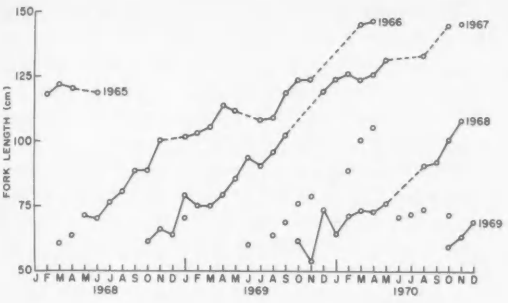

FIGURE 4.—Mean length of size groups of yellowfin tuna as a function of sampling date at Dakar. Growth of the 1965-69 year classes are indicated.

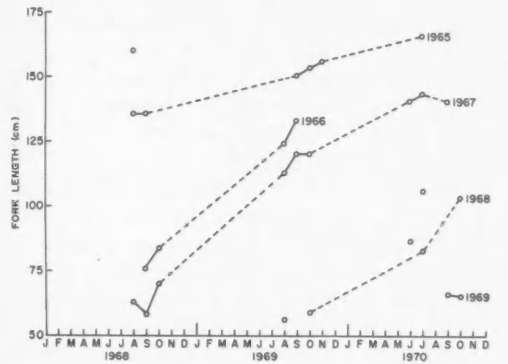

FIGURE 5.—Mean length of size groups of yellowfin tuna from the Gulf of Guinea. Growth of the 1965-69 year classes are indicated.

in some years. Recruitment is assumed to be completed in the second year of life (Le Guen et al., 1969).

RESULTS

Recruitment

Yellowfin tuna are recruited into the surface fishery when about 60 cm long. Recruitment is year-round but most pronounced during June to December. Two groups of yellowfin tuna appear to be recruited in some years. For example, in 1968 at Pointe-Noire (Figure 6) one group entered in January and another in August-September. The January group was of low relative abundance and persisted up to a length of about 90 cm, while the August-September group was of high relative abundance and discernible up to a length of about 140 cm. A similar phenomenon was described by Hennemuth (1961) and later verified by Davidoff (1963) for yellowfin tuna of the eastern Pacific Ocean. Hennemuth suggested that sampling bias, differential growth in a year class, and multiple spawning were some possible causes of the phenomenon. Variation in the seasonal distribution of fishing effort can be added as another possible cause.

Year Class Difference in Apparent Growth

Estimates of apparent growth for individual year classes for each region are shown in Table 3.

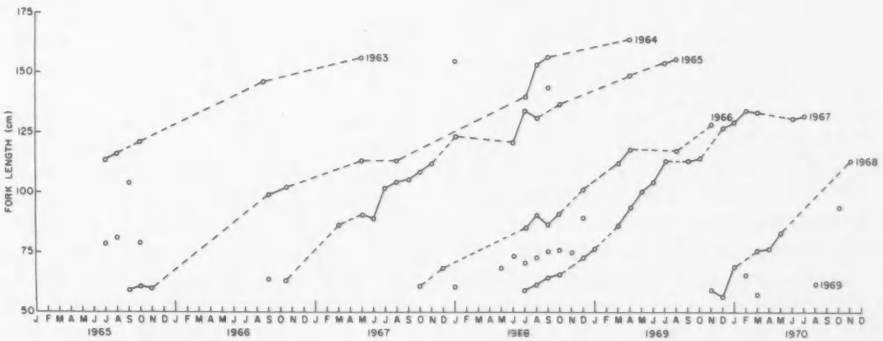
FORK LENGTH (cm)
1963
1964
1965
1966
1967
1968
1969
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1965
1966
1967
1968
1969
1970

FIGURE 6.—Mean length of size groups of yellowfin tuna as a function of sampling date at Pointe-Noire. Growth of the 1963-69 year classes are indicated.

TABLE 3.—Estimates of parameters of the von Bertalanffy growth function for yellowfin tuna of unknown age from the eastern Atlantic Ocean.

Region	Year class	L_∞	K	No. of observations	Range of lengths (cm)
Abidjan	1963	Linear		2	97.2-156.6
	1964	138.6	0.137	9	80.7-149.7
	1965	275.2	0.016	11	59.2-153.6
	1966	Linear		9	62.9-148.4
	1967	155.1	0.086	13	69.4-143.7
	1968	Linear		4	67.9-105.6
	All years	185.0	0.043	48	59.2-156.6
Dakar	1965	Linear		2	117.9-122.3
	1966	Linear		18	70.1-147.2
	1967	201.5	0.038	20	62.3-146.3
	1968	557.2	0.008	11	53.2-108.8
	All years	307.9	0.017	51	53.2-147.2
Gulf of Guinea	1965	677.4	0.002	5	135.8-165.7
	1966	497.5	0.009	3	77.0-132.6
	1967	174.4	0.052	8	57.8-143.3
	1968	Linear		2	56.8- 87.1
	All years	185.0	0.041	18	56.8-165.7
Pointe-Noire	1963	168.3	0.067	5	104.0-155.9
	1964	273.9	0.017	10	59.1-164.8
	1965	162.9	0.059	16	63.0-156.0
	1966	191.9	0.024	11	61.4-127.7
	1967	160.2	0.051	17	59.7-134.7
	1968	177.8	0.033	8	56.6-113.5
	All years	210.1	0.027	67	56.6-164.8
All regions	1963	158.5	0.136	7	97.2-156.6
	1964	237.4	0.023	19	59.1-164.8
	1965	191.0	0.034	34	59.2-165.7
	1966	895.7	0.003	41	61.4-148.4
	1967	172.6	0.054	58	57.8-146.3
	1968	502.4	0.009	25	53.2-113.5
	All years	194.8	0.035	184	53.2-165.7

In some instances, the estimates of K and L_∞ are unexpectedly too high or too low, indicating that the estimates are inappropriate for the entire life span of the species. According to Knight (1968) and Le Guen (1971), a possible cause of variation in K and L_∞ is lack of size measurements for the entire life span of the species. This appears to be the case in some instances for our data. Length measurements for Dakar, for example, were from catches made predominantly by pole-and-line, or baitboats that generally catch small fish, a characteristic that is well documented (Pianet and Le Hir, 1971). Consequently, large fish were underrepresented in the samples, resulting in heavier weight on the lower size groups. Estimates of L_∞ were therefore unreasonably high, while those of K were unreasonably low. It should be noted that generally L_∞ and K are inversely correlated (Beverton and Holt, 1959).

For some year classes, apparent growth appears to be exceptionally faster than for others. Apparent growth of yellowfin tuna from Pointe-Noire can best illustrate this point (Figure 6). The 1965 and 1967 year classes grew at a faster rate than the 1964 or 1966 year class. The result was an apparent convergence of the growth curve for the 1964 year class with that for the 1965 year class, and the 1966 year class with the 1967 year class. In each case, there appears to be no relation between the time of recruitment and the rate of growth.

Regional Differences in Apparent Growth

For each region, the von Bertalanffy equation was fitted to data for all year classes combined. Apparent growth of yellowfin tuna from Abidjan, Gulf of Guinea, and Pointe-Noire was quite similar for sizes (ranged from about 60 to 160 cm long) observed in the samples (Figure 7). Apparent growth of Dakar fish, on the other hand, seemed exceptionally faster, which is at-

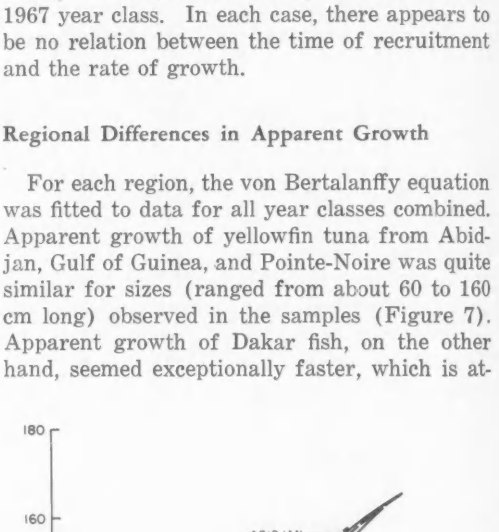

FIGURE 7.—Growth of yellowfin tuna from the eastern Atlantic Ocean.

tributed to lack of data on older fish as was discussed earlier. The range of mean length is 50 to 150 cm.

Estimated Length at Age

An estimate of $L_\infty = 194.8$ cm, and $K = 0.035$, on a monthly basis, was derived from data for all year classes and regions combined (Table 3). We believe these estimates are the "best," on the average, for yellowfin tuna of the eastern Atlantic Ocean, because they were based on data from a broad geographic area off Africa and a wide range of sizes. The estimated growth curve is quite similar to that for Abidjan, Gulf of Guinea, and Pointe-Noire (Figure 7). For individual year classes, however, estimates of L_∞ and K can be expected to deviate from the average, since there is an apparent difference in apparent growth among year classes (Table 3) and considerable scatter of observed mean lengths around the average curve (Figure 8).

Data on growth of tagged yellowfin tuna in the eastern Pacific and on the time of spawning in the Atlantic were used to estimate t_0 in months. The above best estimates of parameters of the von Bertalanffy equation were then used to estimate the length of yellowfin tuna at particular ages. A tacit assumption of this method of estimating length at age is that the von Bertalanffy function is a valid growth model for yellowfin tuna, and the date of birth is constant.

Schaefer, Chatwin, and Broadhead (1961) reported that yellowfin tuna of 40-49 cm long at tagging grew at a rate of 33 cm/year. They indicated that growth was probably adversely affected by tagging, implying that their estimate was too low.

Le Guen et al. (1969) reviewed the literature on time of spawning of yellowfin tuna in the Atlantic Ocean. They concluded that spawning occurred primarily at temperatures greater than 26°C and salinity of about 33.5‰. From seasonal distributions of temperature, salinity, and tuna larvae captured off Africa, they estimated that spawning peaked on about March 1 off Pointe-Noire and on about July 1 off Dakar.

From the above information together with the fact that recruitment into the surface fishery is generally from June to December, we estimated that yellowfin tuna were, on the average, 18 months old at recruitment, about 60 cm long, and $t_0 = 7.48$. Estimates of length at age were calculated with $L_\infty = 194.8$, $K = 0.035$, and $t_0 = 7.48$, employed in the von Bertalanffy function (Table 4). The estimates are graphed in Figure 8, together with monthly mean lengths of individual year classes of each region. There is considerable scatter of the data about the line and an indication that lengths at age 50 months and older are overestimated.

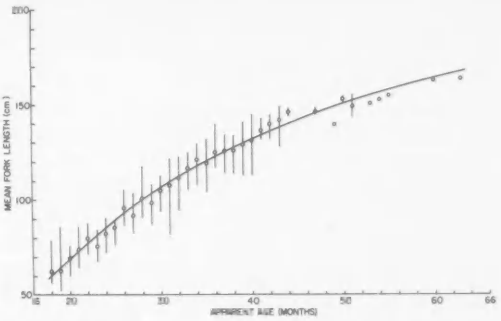

FIGURE 8.—Mean length of year classes of yellowfin tuna as a function of age. The curve is for all year classes and regions combined and is estimated by a von Bertalanffy growth function. Average of observed mean lengths (circles) and the range of mean lengths (vertical line) at various estimated ages are shown.

Estimated Weight at Age

Length can be converted to weight with a weight-length relation. Lenarz (see footnote 4) reported that the weight-length relation for yellowfin tuna from the eastern Atlantic is $W = 0.0000214\ L_f^{2.9736}$, where W = weight in kilograms and L_f = fork length in centimeters. This equation was employed to convert estimates of length at age to weight at age (Table 4).

ANALYSIS WITH APPARENT KNOWN AGE FISH

METHODS

The method of analysis with apparent known

TABLE 4.—Observed and estimated size at various ages of yellowfin tuna from the Atlantic and Pacific Oceans. Length (cm) is shown for most ages, and weight (kg) in parentheses for a few ages. Estimated length is based on the von Bertalanffy growth function.

Age (years)	Source of data											
	Yang et al., 1969		Le Guen et al., 1969				Present study				Davidoff, 1963	
	Atlantic Ocean		Eastern Atlantic				Eastern Atlantic				Eastern Pacific	
			Pointe-Noire		All regions		São Tomé-Angola		All regions			
	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated
1.0	--	54.0	--	33.2	--	32.2	--	17.3 (0.1)	--	28.5 (0.4)	--	34.6
1.5	66.1	75.8	64.6	62.9	63.8	60.0	61.5	53.9 (3.0)	62.2	60.0 (4.2)	--	61.9
2.0	86.1	94.9	84.6	86.6	79.5	83.1	77.6	82.0(10.5)	82.3	85.5(11.9)	83.0	84.7
2.5	104.1	111.5	108.3	105.6	103.9	102.0	111.0	103.6(21.1)	105.0	106.2(22.7)	105.0	103.8
3.0	120.0	125.9	--	120.9	124.0	117.7	116.1	120.2(32.8)	125.0	123.0(35.1)	122.0	119.7
3.5	132.9	138.5	132.2	133.1	132.2	130.6	132.2	133.0(44.3)	140.6	136.6(48.0)	136.0	132.9
4.0	--	149.4	--	142.9	--	141.3	135.6	142.8(54.7)	--	147.6(60.5)	141.0	144.0
4.5	--	158.9	147.0	150.7	143.6	150.1	147.0	150.3(63.8)	153.4	156.6(72.0)	--	153.3
5.0	--	167.2	152.0	157.0	152.0	157.4	153.7	156.1(71.3)	164.8	163.8(82.4)	--	161.0

age fish were similar to those described by Le Guen et al. (1969) and are briefly described as follows. Predorsal length-frequency distributions were tabulated for monthly samples collected in 1967-71 off Pointe-Noire in an area from São Tomé to southern Angola. Modes were selected by comparison of successive maxima in the length-frequency distributions and mean predorsal length estimated for each size group by a method described by Gheno and Le Guen (1968). Mean dorsal lengths were then converted to fork lengths with the aid of Table 5, which was based on fish measured for both predorsal and fork lengths at Pointe-Noire. The data in Table 5 give a fork length-predorsal length relation of $\log L_f = 0.299 + 1.162 \log L_d$ that is not significantly different from the equation used earlier.

TABLE 5.—Predorsal length and fork length measurements of yellowfin tuna landed at Pointe-Noire, 1967-71.

Predorsal length (cm)	Mean fork length (cm)	Number of observations	Predorsal length (cm)	Mean fork length (cm)	Number of observations
12	39.0	11	31	109.5	46
13	40.9	21	32	111.3	33
14	45.0	18	33	116.1	27
15	47.3	37	34	118.8	19
16	50.0	36	35	122.9	26
17	53.9	33	36	132.3	24
18	57.2	58	37	134.7	35
19	59.8	83	38	138.4	25
20	63.1	66	39	143.7	28
21	66.3	43	40	145.7	29
22	71.0	20	41	149.7	29
23	74.6	23	42	152.3	14
24	76.0	18	43	158.8	5
25	81.1	16	44	164.0	5
26	84.2	16	45	166.3	10
27	89.0	9	46	172.0	6
28	92.8	21	47	175.4	8
29	99.1	28	48	177.8	7
30	104.9	27	49	179.8	2

An estimated age was assigned to each size group (Table 6) based on: (1) date of birth of yellowfin tuna caught off Point-Noire is on the average March 1 and (2) recruitment occurs in the second year of life (Le Guen et al,. 1969). Estimates of parameters of the von Bertalanffy function were then calculated with Psaropolos' (1966) computer program.

Length at age estimates were converted to weight at age with the weight-length relation of Lenarz (see footnote 4), which was mentioned earlier.

RESULTS

Estimates of parameters of the von Bertalanffy function were $L_\infty = 175.17$ cm (SE = 3.67), $K = 0.044$ per month (SE = 0.003), and $t_0 = 9.643$ months (SE = 0.815). These estimates are quite similar to those derived by Le Guen et al. (1969) for the Pointe-Noire region based on only data from 1967-68 (Table 7); but L_∞ is significantly lower and K significantly higher than our best estimates for yellowfin tuna from a larger area of the eastern Atlantic, even when the difference in range of lengths in the data is taken into account. On the other hand, length at age and weight at age estimates for ages 1-5 years are quite similar to those for the entire eastern Atlantic (Table 4). Thus, we conclude

TABLE 6.—Size classes (cm) of yellowfin tuna identified in samples from São Tomé to southern Angola. Year classes are separated by horizontal lines.

Age (months)	1967-68[1]	1969	1970	1971
18	64.5		58.5	
19			59.8	
20			61.4	
21	70.3			
22	85.0	75.3	68.6	58.5
23	85.1		71.0	63.1
24	84.6	82.6	74.6	68.6
25	89.0	90.9	81.1	72.8
26	90.6	104.9	82.6	74.6
27	91.0	107.2	92.8	76.0
28	95.5	107.2		86.6
29	102.6			
30	108.3	113.7		
31	107.7	116.1		
32	109.4	127.5		
33	114.5	127.5		
34	124.0			
35	120.0	111.3		
36		116.1		
37	122.0	118.8		
38	126.7			
39	123.5			
40	134.7			
41	136.8			
42	132.2			
43	139.0			
46			133.5	
47	138.6			
48			136.5	134.7
52	147.0		141.0	138.4
53	151.3		143.7	
54	147.0			
55	150.5			
60	152.0			155.5
61		149.7		156.0
64				158.8
65	163.4			160.0
66	161.9			
73		166.3		
74		168.1		
75		168.0		170.1
76				170.1
77				170.1

[1] Data from Le Guen et al. (1969).

that there is no appreciable difference in the estimate of apparent growth of yellowfin tuna from the region of the eastern Atlantic, illustrated in Figure 1 or from a smaller region within that part such as off Pointe-Noire.

COMPARISON OE GROWTH ESTIMATES

Studies on growth of yellowfin tuna have largely been based on two types of data: length-frequency distributions and scale readings. For comparative purposes we chose two studies that were based on scale readings—one each from the Pacific (Yabuta, Yukinawa, and Warashina, 1960) and Atlantic (Yang et al., 1969)—and three studies that were based on modal progression of length-frequency distributions—two from the Pacific (Davidoff, 1963; Moore, 1951) and one from the Atlantic (Le Guen et al., 1969)—for comparison with our best estimates for the eastern Atlantic. The procedure of estimating the parameters of the von Bertalanffy function was standardized with the use of the Fabens' (1965) procedure whenever appropriate data were available.

ESTIMATES FROM SCALE READINGS

Lengths at mark formation from interpretation of marks on scales were reported by Yabuta et al. (1960). They indicated that mark formation occurs twice a year, in March-April and in September-October, or 6 months apart in the western Pacific. An estimate of growth was calculated from their data with 6 months between marks (Table 7). Growth appears to be substantially slower in the western Pacific than in the eastern Atlantic (Figure 9). Either growth is indeed slower in the western Pacific or the interpretation of scale marks by Yabuta et al. is in error. The latter possibility is suggested by the absence in their data of fish greater than 119 cm long with a designated mark, although fish as large as 161 cm long were reportedly sampled. Moreover, only about 42% of their scales were readable. Other studies made in the western Pacific (see Shomura, 1966; Suzuki, 1971) suggest that growth was underestimated by Yabuta et al.

$L_\infty = 222.8$ cm and $K = 0.023$, on a monthly basis, were estimated by Yang et al. (1969). Their estimates were based on scale readings of 296 yellowfin tuna caught by the Atlantic long-line fishery. Since Yang et al. used the Walford (1946) procedure to estimate growth, we recalculated growth with the Fabens' procedure using the data of Yang et al. and the assumption that the scale marks formed every 6 months. The results (Table 7) were not markedly different from the estimates by Yang et al. Compared to our best estimate of growth rate (K), on the other hand, their estimate is substantially

TABLE 7.—Estimates of parameters of the von Bertalanffy growth function for yellowfin tuna from the Atlantic and Pacific Oceans. Estimates are based on data reported in various studies, and were calculated by Fabens' (1965) procedure, except those of Le Guen et al. (1969).

Region	L_∞	K	Range of length (cm)	Source of data	Data
Atlantic Ocean	223.0	0.023	66-133	Yang et al., 1969	Scale readings; Table 6
Eastern Atlantic				Le Guen et al., 1969	Length frequencies; estimates reported by authors
Dakar	206.6	0.026	63-162		
Pointe-Noire	182.4	0.037	64-162		
All areas	191.7	0.032	63-162		
Eastern Atlantic				Present study	Length frequencies (Age unknown)
Abidjan	185.0	0.043	59-157		
Dakar	307.9	0.017	53-147		
Gulf of Guinea	185.0	0.041	57-166		
Pointe-Noire	210.1	0.027	57-165		
All areas	194.8	0.035	53-166		
Eastern Atlantic				Present study	Length frequencies (Age known)
São Tomé-Angola	175.2	0.044	58-170		
Central Pacific	191.9	0.036	47-168	Moore, 1951	Length frequencies; Table H
Eastern Pacific	200.3	0.030	69-148	Davidoff, 1963	Length frequencies; Table 6
Western Pacific				Yabuta et al., 1960	Scale readings; Table 5
Males	202.1	0.023	58-119		
Females	174.9	0.031	57-119		
All sexes[1]	188.4	0.027	57-119		

[1] Estimates were based on weighed average length for each scale mark reported by Yabuta et al. (1960). Sample size of each sex was used as the weighing factor.

smaller. Possibly this smaller K is caused by error in the interpretation of scale marks and the paucity of large fish in their data. The maximum number of marks observed by Yang et al. was five, with a corresponding mean length of 132.9 cm at time of fifth mark formation, but fish as large as 180 cm long were reportedly sampled. For our study, fish as large as mean length 166 cm were used in the calculations.

ESTIMATES FROM MODAL PROGRESSION

Davidoff (1963) examined modal progressions of length-frequency distributions of eastern Pacific yellowfin tuna caught by baitboats and purse seiners and calculated with the Walford procedure $L_\infty = 167$ cm and $K = 0.05$, on a monthly basis, which he noted were similar to earlier estimates reported by Hennemuth (1961). Davidoff's estimates were based on average modal length at each age of all year classes combined. Equal weight was therefore given to each datum point in his calculation.

Using the Fabens' procedure and data for each year class reported by Davidoff (his Table 6), we recalculated the growth estimates. The results, $L_\infty = 200.3$ and $K = 0.030$, are considerably larger for L_∞ and smaller for K than Davidoff's estimates but similar to our estimates for Atlantic yellowfin tuna (Table 7).

Hennemuth (1961) reported that fish 70 cm long in the eastern Pacific were about 20 months old. Entered into the von Bertalanffy equation, this gives a t_0 of 5.67 months with $L_\infty = 200.3$ and $K = 0.030$, and a means of estimating length at age for eastern Pacific yellowfin tuna. The results are shown in Table 4. They compared favorably with our estimates for Atlantic yellowfin tuna, although apparent growth in the eastern Atlantic is 0.9 to 2.8% faster than that in the eastern Pacific for ages 2 through 5 years.

Moore (1951) based his estimates of growth on length-frequency distributions of yellowfin tuna caught primarily by longline gear in the central Pacific. He used the Walford procedure and calculated $L_\infty = 190.0$ cm and $K = 0.037$ per month. Because of a limitation of Walford's

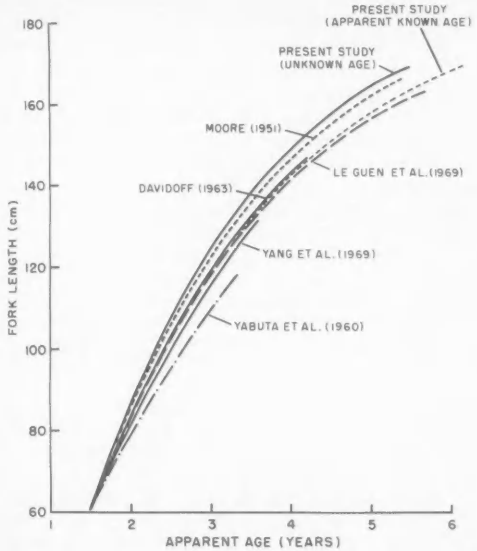

FIGURE 9.—Comparison of growth of yellowfin tuna from the Pacific and Atlantic Oceans. Curves were adjusted to a common base of age 1.5 years = 60 cm long and were estimated, except for that of Le Guen et al. (1969), from data reported in various studies.

method—requiring length measurements at equal time intervals—Moore was able to use only 16 out of his 25 observations. We recalculated L_∞ and K, using the Fabens' procedure and the 25 observations reported by Moore (his Table H). The estimates, $L_\infty = 191.9$ and $K = 0.036$, differ slightly from those of Moore and are very similar to our estimates for Atlantic yellowfin tuna.

Le Guen et al. (1969) estimated growth of yellowfin tuna from Dakar, Pointe-Noire, and both regions combined, based on modal progression of length-frequency samples (Table 7). Their samples were identical to some used in our study, but their estimate of growth for combined regions is slightly lower than ours; the difference in estimated lengths for ages 2 through 5 years is 2.8 to 4.3% less (Table 4). Part of the difference is in the method of analysis. The estimates by Le Guen et al. were based on mode selection from predorsal length distributions, and the lengths of size groups were not assumed to be normally distributed. Predorsal lengths were then converted to fork length; whereas in our best estimate predorsal length was converted to fork length by a log function before frequency distributions were analyzed, and the lengths of size groups were assumed to be normally distributed. Furthermore, Le Guen et al. assumed that the date of birth of fish of each year class of a region was the same and accordingly ages were assigned to size classes; such an assumption was not made for our estimate of K and L_∞; but for obtaining t_0 we assumed that yellowfin tuna of 60 cm long are 18 months old. Nevertheless, the difference is insignificant in view of the fact that there is considerable variability in observed mean lengths at age (Figure 7).

DISCUSSION

It is obvious from the results that estimates of growth of yellowfin tuna are quite variable and largely dependent on the method of analysis. Both the length-frequency and scale methods are based on various assumptions that are not always satisfied. For example, the assumption in the length-frequency method that size groups represent age groups, and the age groups are formed once a year, i.e., hatching within a short period, or season, is not completely satisfied for yellowfin tuna, since spawning occurs over several months (Matsumoto, 1966; Le Guen et al., 1969; Richards, 1969). Nevertheless, in many areas, as in the eastern Atlantic, there is generally a peak month of spawning (Le Guen et al., 1969) that can create a size group discernible in size-frequency distributions in later dates.

The scale method assumes that the scale marks are formed at regular intervals. So far, this assumption has not been satisfactorily verified for yellowfin tuna, although Yabuta et al. (1960) and Yang et al. (1969) have indicated that the marks formed every 6 months. Furthermore, because yellowfin tuna generally spawn over an extended season, the age at first annulus formation is not the same for all individuals of a year class. The back-calculated length at age I may therefore be questionable. It is surprising, however, that the observed lengths at age are remarkably similar for studies based on the scale and length-

frequency methods (Table 4). This suggests that the marks on scales of Atlantic yellowfin tuna are indeed layed down at regular intervals and that observed lengths at age rather than estimates of parameters of the von Bertalanffy function are more meaningful in comparison of growth of yellowfin tuna. For such a comparison, the average growth rate of Atlantic yellowfin tuna is 17 cm/6 months, based on the scale method, and 18 cm/6 months, based on the length-frequency method for ages 1.5-3.5 years.

The comparison of observed lengths at age also indicates that there is little difference between growth of Atlantic and Pacific yellowfin tuna (Table 4). Yang et al. (1969), on the other hand, suggested that growth is faster in the Atlantic than in the Pacific. We analyzed their data with analysis of covariance and found that their Walford curves for the Atlantic and Pacific yellowfin tuna were not significantly different from a common line ($F_{2,5} = 0.474$) nor from parallel lines ($F_{1,5} = 0.904$). Thus the suggestion by Yang et al. was not demonstrated by their data, but in fact, growth of yellowfin tuna appears to be similar in the two oceans.

Finally, since the parameters of the von Bertalanffy growth function are sensitive to the method of analysis and range of sizes used to estimate them, we recommend that the observed size at age rather than the estimated size at age from the von Bertalanffy growth function be used in estimating yield per recruitment. The Ricker (1958) model of yield per recruitment, for example, is appropriate for observed values.

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DESCRIPTIONS OF THE LARVAE OF FOUR NORTH PACIFIC PORCELLANIDAE (CRUSTACEA: ANOMURA)[1]

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ABSTRACT

Complete descriptions are given of the zoea and megalopa stages of four porcelain crabs common in the rocky intertidal regions of the Pacific coast of North America. Both larvae reared in the laboratory and larvae taken from the plankton were available for the species *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles pubescens* Holmes, and *Pachycheles rudis* Stimpson. All four species have a short prezoea stage, two zoeae, and a planktonic megalopa stage. Extensive variation was found in setal numbers between left and right members of appendage pairs and between individuals in these larvae. Setal counts characteristics of species cannot be obtained from one or a few larvae, and ranges in the counts overlap considerably between species. The criteria of Lebour for grouping zoeal types in the Porcellanidae are applied to these four species and comparisons made between all available descriptions of porcellanid larvae. Intermolt growth of appendage buds occur in these four species, and it is concluded that this type of growth is the cause of most of the differences described previously as larval substages. Tabulations of species showing stage variation and intermolt growth are given.

All larval stages of four common Pacific coast rocky intertidal porcelain crabs have been reared in this laboratory. Material obtained from cultures and from the plankton was used for the descriptions given here of the larvae of each species. One of these species, *Pachycheles rudis*, has been described previously (Knight, 1966), and in this case the available material permitted this description to be expanded. Attention was also directed to variation in larval characteristics since adequate numbers of specimens were available for examination.

Gravid female porcelain crabs of the species *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles rudis* Stimpson, and *Pachycheles pubescens* Holmes were collected from rocky intertidal shores at Boiler Bay and Yaquina Head on the central Oregon coast. *P. rudis* was collected from the lower intertidal (—0.8 to —2.5 ft below mean lower low water) beneath *Phyllospadix* root mats on the seaward sides of large boulders. *Pachycheles pubescens* was collected from burrows and crevices in rock at the same tide level. The *Petrolisthes* species were gathered somewhat higher in the intertidal regions of the two sites beneath loosely bedded rocks and rubble. All four species occur in various other habitats as well (Haig, 1960) but were taken from these areas for convenience. Egg-carrying *Pachycheles rudis* were collected in May and June of 1968. In the same months of 1969, egg-bearing females of the other species were obtained for larval studies. Gravid females were also noted during other months of the year, in agreement with Knudsen's (1964) observations on the reproductive cycles of these species. The specific identity of the females used was confirmed by comparing them to the descriptions given by Haig (1690).

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Female crabs were held individually in 1-liter beakers containing 600 ml of aerated, unfiltered seawater, standing in trays of running seawater ranging in temperature from 10.8° to 15.2°C. The water in the beakers was changed every 2 days. Larvae released by the females were removed from the beakers as soon as a hatch was discovered. Only actively swimming larvae of normal appearance were used.

Glassware for handling and culturing larvae was washed in fresh water, rinsed with distilled water, and steam autoclaved to minimize microbial contamination of the cultures. Seawater used for culturing was collected at high tide from the laboratory seawater system, passed through a sintered glass filter of pore size 40-60 mμ, and stored at 9°C in darkness. The salinity of this water ranged from 32.8 to 33.7‰.

Laboratory-hatched larvae of *Pachycheles rudis* and *Petrolisthes eriomerus* were cultured in flasks, while *P. cinctipes* larvae were reared in mass cultures only. Larvae from a single *Pachycheles pubescens* female were divided between flask and mass cultures. Light received by the larvae was not controlled. In all flask cultures larvae were maintained without aeration, initially with six to eight zoea I larvae per Erlenmeyer flask. The seawater volume allowance ranged from 25 ml per larva for early stages to 50 ml per larva for the larger later stages. Flasks were maintained at either 12°C or 15°C (± 0.01°C) in refrigerated baths of circulating water. All flask cultures were examined daily, mortality recorded, and newly molted larvae transferred to new cultures. Plankton tows were made intermittently from May through September of 1968 in Yaquina Bay and 1 mile outside the estuary along a rocky reef paralleling the shore. The catch was immediately resuspended in cold seawater and kept under refrigeration while being taken to the laboratory. Live porcellanid larvae obtained in these hauls were removed to fresh seawater, sorted by zoeal stage, and further separated into four groups on the basis of differences in the patterns of the primary red chromatophores. Larvae within each group were further divided and placed in flask cultures.

Mass cultures of laboratory-hatched *Petrolisthes cinctipes* larvae were maintained in 5-gal carboys filled with filtered seawater, with 150 or fewer larvae per carboy. Aerated mass cultures were immersed in baths of running seawater and experienced a temperature range of 10.8° to 15.2°C during the culture period and a maximum daily fluctuation of 2.5°C due to tidal influence. Larvae in mass culture were transferred to clean containers and fresh seawater every 14 days.

Zoea larvae were fed *Artemia salina* nauplii not more than 3 days old daily if required so that excess food was always present. The megalopa larvae required suspended algal material as food. Several monoalgal (*Tetraselmis* sp., *Isochrysis* sp.) and diatom (unidentified) cultures were tried singly and in combinations as a food source. Nutrient culture medium inoculated with raw seawater was also used as a source of food organisms. Small stones were introduced into the flasks to provide the megalopae with a surface for settling.

The larvae of the two *Petrolisthes* species and *Pachycheles rudis* were reared to the megalopa stage in cultures from embryos obtained from females held in the laboratory. Live larvae of these species taken from the plankton were reared to confirm stages obtained from the laboratory-hatched broods and to supplement laboratory-grown material for descriptive purposes. The larval history of *P. pubescens* was first described from larvae captured in the plankton and placed in laboratory cultures. Three gravid females of this species were collected later, and the identity of the planktonic larvae was confirmed by comparison with larvae released by one of the females and reared to the second zoeal stage.

Larvae in various stages of development were preserved for dissection primarily in 70% ethanol, but a few larval specimens were preserved in a mixture of 50% glycerine and 50% ethanol for chromatophore examinations. Both temporary and permanent slides were made of the dissected materials. Temporary mounts were made in glycerine, and permanent mounts were made in Zeiss hardening phase medium as well

as in Turtox CMC-9AB and CMC-10 media.[3] Drawings were made from both types of material with the aid of a Wild M-20 compound microscope and camera lucida attachment. Since the length of the rostral and posterior spines of zoeae is highly variable and dependent on a number of factors, only the carapace proper was measured to serve as an indication of zoeal size. This measurement was made from the point of junction of the posterior spines to the posterior margin of the orbital arch, using an ocular micrometer.

The term "seta" is used to indicate any firm-walled process, located on an appendage or other body surface, which is distinctly articulate at its base or attachment point (Figure 1). The figures are in part schematic and represent typical setal counts only. Setules are not represented in actual numbers and are often omitted entirely for clarity. Only one member of each setal pair present is figured for the exopodites of zoeal maxillipeds. Only the right member of each appendage pair is figured except for mandibles, which are sometimes drawn in pairs from the dorsal view.

Sexually mature females of the two genera considered in this study produce eggs of distinctly different types. *Pachycheles rudis* and *P. pubescens* females carry eggs which are 0.50 to 0.58 mm in size and brilliant yellow-orange when they are newly extruded. The eggs of *P. rudis*, as Knudsen (1964) and Knight (1966) observed, gradually change to a translucent amber color as the embryos develop and the yolk is absorbed. The color change with development is similar in *P. pubescens*. The age of the egg masses of the individual females collected in the field was unknown; however, the maximum length of time any female *P. rudis* carried eggs was 47 days, and two others carried eggs for 43 days before releasing larvae. This time may approach the length of time eggs are carried in this species. In both *Pachycheles* species, eggs hatched and all the larvae were released in a period of 10 to 20 hr. A hatch from a large female (carapace width 14.2-15.0 mm) may yield between 2,000 and 3,000 larvae but brood size varies (Knudsen, 1964).

In contrast, the eggs of *Petrolisthes cinctipes* and *P. eriomerus* are somewhat larger, 0.80 to 0.84 mm, and are deep scarlet to maroon in color, when newly extruded, similar to those of other species in the genus (Wear, 1965b; Greenwood, 1965). As Boolootian et al. (1959) also observed, the eggs gradually change to a translucent brownish red color as the embryos develop and the yolk is absorbed. Females of these two species were deliberately collected close to the hatching time; consequently, no information on the length of the brooding period was obtained. The time required for a female to complete a hatch is similar in these two *Petrolisthes* species but differs considerably from that observed for the *Pachycheles* species. Female *Petrolisthes* require 40 to 70 hr to release an entire group of larvae in the laboratory. Release of the larvae in these two species occurs in spurts with "resting" periods between each period of concentrated release.

The embryonic and larval histories of all four species observed in the laboratory have a number of characteristics in common. Fully developed embryos examined prior to eclosion possessed the full complement of primary red chromatophores found throughout the active larval life of these crabs. Although occasional minor variations were noted both in laboratory hatches and in larvae from the plankton, the occurrence and placement of the chromatophores is generally stable and is species specific, as various workers have noted in other species (Wear, 1964a, b, 1965a, b; Greenwood, 1965; Gore, 1968; Gurney, 1942). The primary chromatophores can thus be used to identify a larva to the species level at any stage of development.

In the hatching of all four species, females released larvae in the form of prezoeae. This has been observed in other porcellanid species, for example, by Lebour (1943), Greenwood (1965), Wear (1965b, 1966), and Gore (1968). The duration of this stage in the laboratory varies considerably and lasts from 10 min to about 1 hr in the species studied here. Prezoeae were never collected in the plankton.

[3] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

FIGURE 1.—Setal types in four porcellanid species studied: A-E (Scale 1), zoeal telson processes, distal portions: A - processes 3 and 4, *Pachycheles* spp.; B - processes 5, 6, and 7, *Pachycheles* spp.; C - median spine, Zoea II, *Pachycheles* spp.; D - processes 3 through 7, *Petrolisthes* spp.; E - median spine, Zoea II, *Petrolisthes* spp. F-K (Scale 2), zoeal maxillary setae, all four species. L, N (Scale 2), scythelike cleaning setae, straight and hooked, megalopa, pereiopod 5, all four species. M, O (Scale 2), "spikelike" and "brushlike" setae, megalopa, maxilliped III, all four species. Scales in millimeter.

After the larva has spent a period of time as a prezoea, the cuticle over the carapace is ruptured dorsally along the midline and the prezoea molts to the first true zoeal stage. The rostrum is the first portion of the body to be freed, followed by the functional mouth parts and natatory maxillipeds. The abdomen and telson are the last portions to be withdrawn from the cuticle. When the molt is completed, the natatory setae and setae of the telson, previously compacted and confined by the prezoeal cuticle, become fully extended and serve to keep the larva afloat and propel it through the water. The rostral spine, partially invaginated into the carapace in the prezoea, straightens out almost immediately following the molt. The posterior carapace spines which often, but not always, become tightly coiled immediately after the cuticle is shed may take several minutes to several hours to uncoil. The cuticle is shed virtually intact except for the original dorsal split. Often in later molts, the delicate elastic cuticle covering the pereiopod and pleopod buds is shriveled or damaged in the cast exoskeleton.

Larvae of all four species always pass through two true zoeal stages and one megalopal stage (terminology of Williamson, 1957) in the laboratory as do certain other porcellanids (Le Roux, 1961, 1966; Knight, 1966; Boschi, Scelzo, and Goldstein, 1967; Gore, 1968, 1970, 1971a, b, 1972). This was true of larvae hatched in the laboratory as well as those taken from the plankton.

In these four species, both zoeal stages demonstrate the remarkable property of intermolt growth in which certain of the larval appendages increase in size, apparently throughout the duration of a stage, while the larval cuticle remains intact. This phenomenon has been reported for various other porcellanid larvae (Le Roux, 1961, 1966; Kurata, 1964; Knight, 1966; Gore, 1968, 1970, 1971a, b, 1972) but has not yet been thoroughly investigated. Appendages may increase in size as much as threefold between molts as a result of this growth pattern.

The number of specimens of each stage dissected and examined is given in Table 1. The ranges given in the descriptions refer only to variations found within these specimens. Many other specimens were examined but not dissected.

LARVAL DEVELOPMENT OF *PETROLISTHES CINCTIPES* (RANDALL)

Larvae of *P. cinctipes* were reared using the mass culture method. The single megalopa thus obtained as well as one megalopa from the plankton were preserved and dissected for purposes of description.

PREZOEA
(Figure 2)

The prezoea of *P. cinctipes* is virtually spineless and hairless. The carapace has a generally rounded appearance because the rostral and posterior spines are curved downward and inward toward the center of the body. These spines are further compacted by being telescoped and invaginated into their respective portions of the carapace. The natatory setae are nonfunctional, withdrawn into the ends of the maxillipeds, and held in place by the prezoeal cuticle. The primary red chromatophores appear in the following locations: one on either side of the mouth; one distally on the basipodite of each second maxilliped; one distally in abdominal segment number two or between segments two and three; and one on either side of the body between the bases of maxillipeds one and two. The rostrum and posterior spines are tipped with red, and an additional red band appears on the rostrum proximal to the red tip and separated from it by a white or colorless band.

With the exception of the chromatophore numbers and arrangement, the prezoeal stages of the four species do not differ significantly. For this reason, a prezoea will be figured only

TABLE 1.—Number of porcelain crab larvae dissected and examined for this study.

Species	Zoea I	Zoea II	Megalopa
Petrolisthes cinctipes	11	4	2
Petrolisthes eriomerus	16	4	9
Pachycheles pubescens	9	6	9
Pachycheles rudis	12	12	7

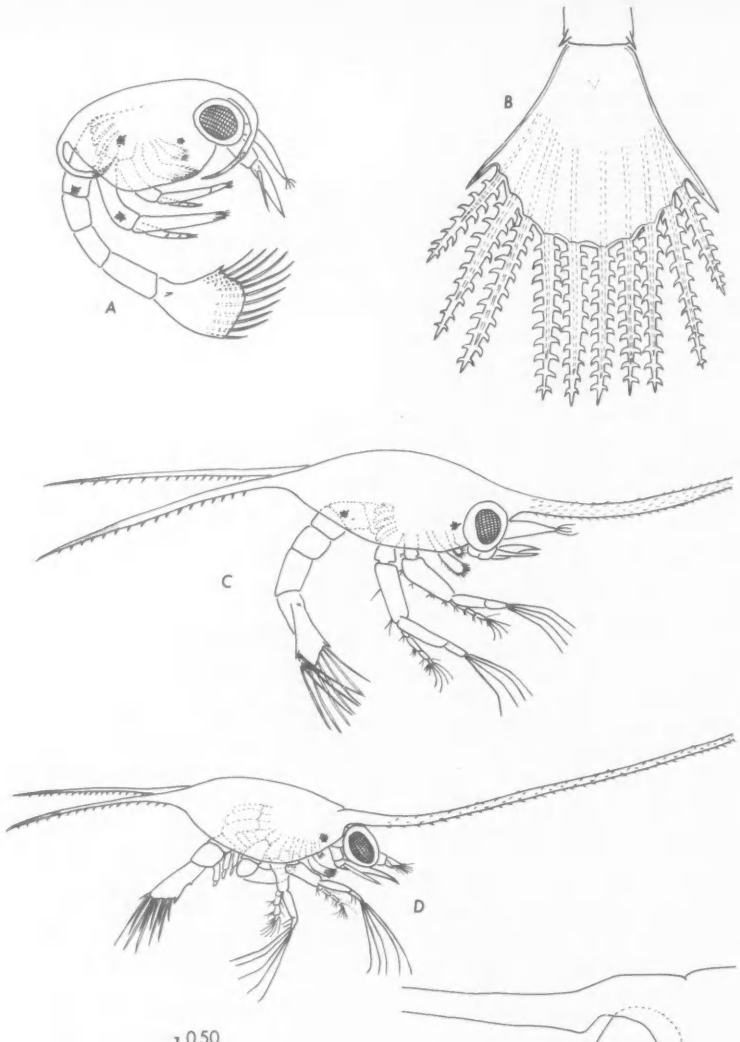

FIGURE 2.—Prezoea, Zoea I, Zoea II, entire: A - prezoea, *Petroli... inctipes* with primary chromatophores (Scale 3); B - prezoeal telson with modified cuticle, *Pachycheles pubescens* (Scale 4); C - *Petrolisthes eriomerus*, Zoea I with chromatophores (Scale 2); D - *Pachycheles pubescens*, Zoea II with chromatophores (Scale 1); E - *Petrolisthes* spp., Zoea II, ventral rostral bulge (Scale 3). Scales in millimeter.

once, and specific variations will be indicated in the text. Prezoeae were not dissected.

ZOEA I
(Figure 3)

Antennule unsegmented with five or six terminal processes including three aesthetascs and two or three setae.

Antenna biramous; endopodite fused with protopodite and bearing a terminal point and subterminal tubercle with a fine seta between; exopodite mobile, about 1½ times as long as endopodite, with three or four prominent distal spines and one long seta proximal to the spines.

Mandibles strongly sclerotized, heavily toothed, asymmetrical appendages.

Maxilla I with unsegmented endopodite bearing three or four terminal setae and a number of fine hairs along the anterior margin; basal endite with 9 or 10 stout spinous processes; coxal endite with 9 or 10 stout setae.

Maxilla II with unsegmented endopodite bearing eight or nine setae, grouped 3, 1-2, 3-4 proximal to distal, 3-2-4 being the most common grouping. Basal endite bilobed: distal lobe with 7 to 10 setae; proximal lobe with seven to nine setae. Coxal endite bilobed: distal lobe with four to six setae; proximal lobe with 8 to 11 setae. Scaphognathite with six or seven long plumose marginal setae, and one apical seta; numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with one or two distal setae. Basipodite with 9 to 11 setae most commonly grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with one to three distal setae, inner margin; segment 2 with two or three distal setae, inner margin; segment 3 with four to seven setae including two or three medial, one or two distal, inner margin, occasionally one long medial seta, outer margin; segment 4 with five to seven terminal setae and one proximal on outer margin. Exopodite two-segmented with four terminal natatory setae on distal segment. Additional groups of very fine hairs appear on endopodite segments 2, 3, and 4 and on segment 2 of exopodite as figured.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with three setae on inner margin grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with one or two distal setae, inner margin; segment 2 with one or two distal setae, inner margin; segment 3 with one medial and one or two distal setae, inner margin; segment 4 with three to five (usually five) terminal setae and one proximal seta, outer margin. Exopodite two-segmented with four terminal natatory setae on distal segment. Groups of very fine hairs appear on endopodite segments 2, 3, and 4 and on both segments of exopodite as figured.

Maxilliped III present as small bilobed bud which undergoes growth throughout stage.

Pereiopods present as five pairs of short limb buds, all without setae; none chelate; undergo growth during entire stage.

Abdominal somites numbering five; segments 3, 4, and 5 with serrated dorsal posterior margins; segments 4 and 5 each with a pair of strong ventrolateral spines on posterior margin.

Telson with seven symmetrically arranged pairs of processes, with central pair located on central prominence; outer margin to center line: one heavy, articulated lateral process with few spinules (not figured), one short fine seta, and five long plumose articulating setae; all long plumose setae armed distally with fixed curved spines (Figure 1D); fine hairs (not figured) on margin of telson between all major plumose setae and on central prominence; anal spine present.

Chromatophores as described in the prezoea; carapace 1.23 to 1.39 mm in length.

ZOEA II
(Figure 4)

Antennule biramous; exopodite with six or seven terminal processes including four aesthetascs and two or three setae, followed by five tiers of subterminal aesthetascs grouped 2, 3, 3, 4, 3 progressing proximally; three or four fine setae present on distal margin of protopodite.

Antenna biramous; endopodite same form as in zoea I; exopodite similar to zoea I, with three spines and one seta distally; exopodite and endopodite approximately equal in length.

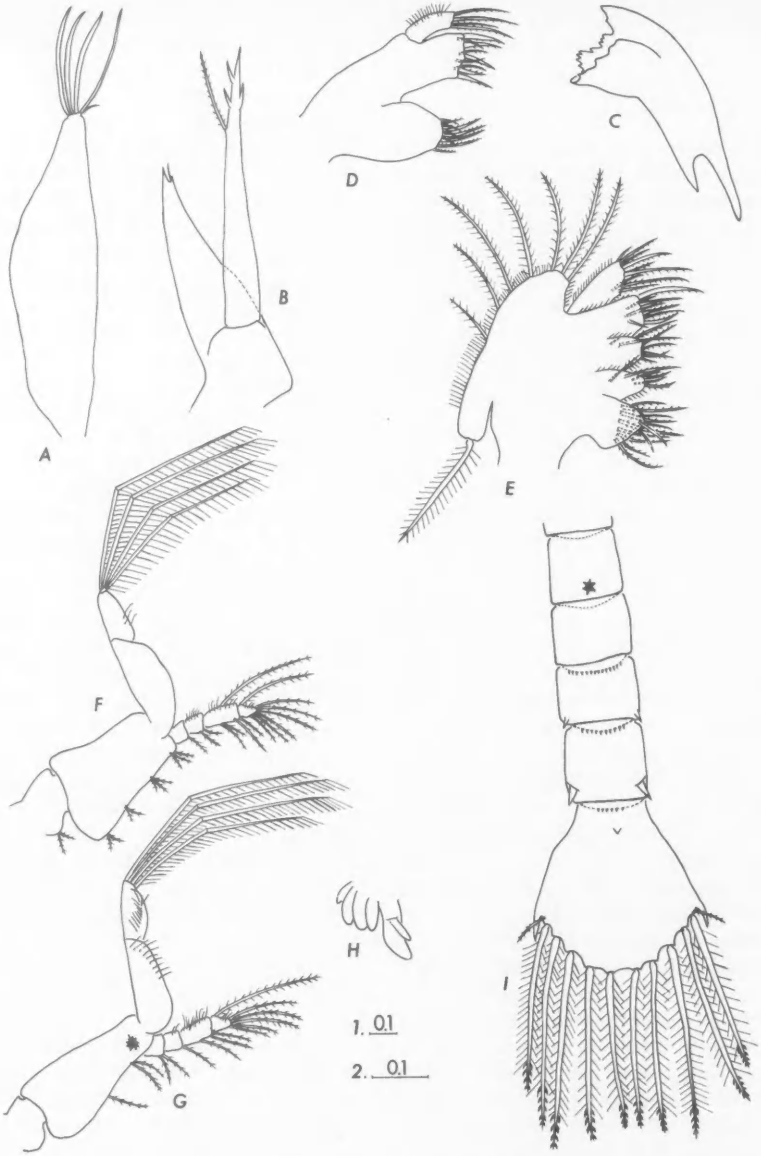

FIGURE 3.—*Petrolisthes cinctipes*, Zoea I: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II (A-E, Scale 2); F - maxilliped I; G - maxilliped II (F and G, Scale 1); H - maxilliped III and pereiopod buds (Scale 2); I - abdomen and telson, ventral (Scale 1). Scales in millimeter.

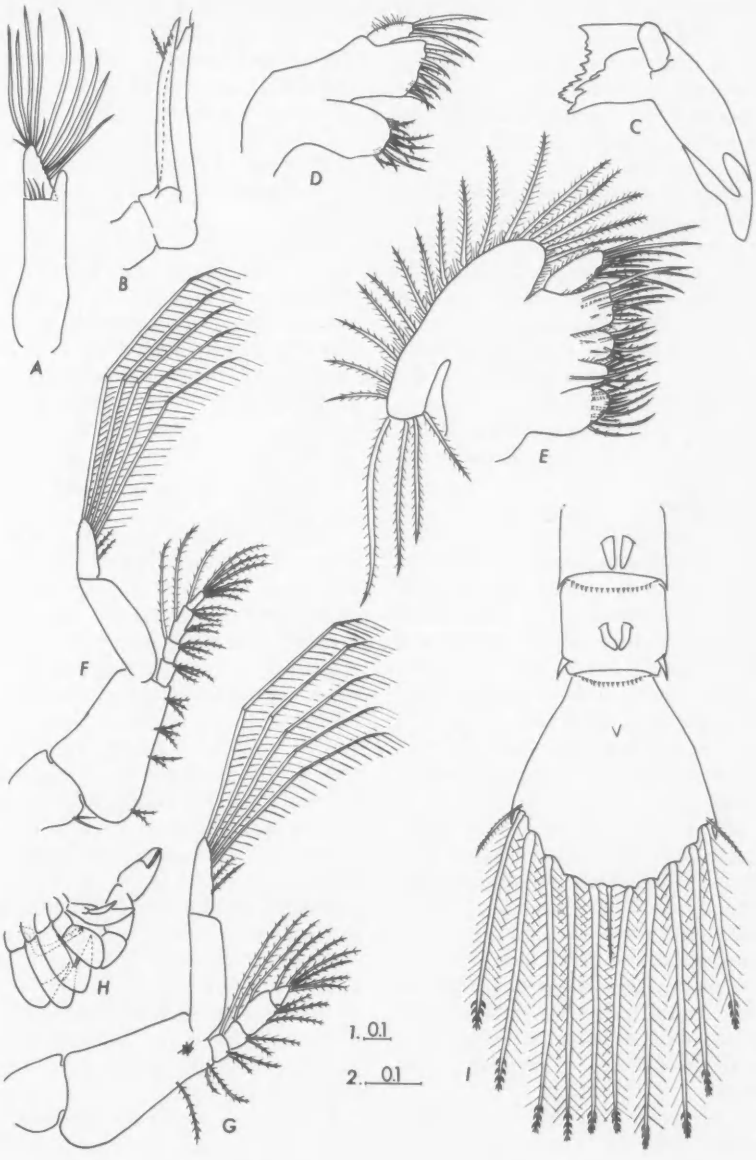

FIGURE 4.—*Petrolisthes cinctipes*, Zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II (A-E, Scale 2); F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopods; I - abdomen and telson (F-I, Scale 2). Scales in millimeter.

Mandibles larger than in zoea I and with prominent palp bud.

Maxilla I with unsegmented endopodite bearing four or five terminal setae and a number of fine hairs along anterior margin; basal endite with 10 or 11 setae; coxal endite with 11 to 13 setae.

Maxilla II with unsegmented endopodite bearing nine setae grouped 3, 2, 4 progressing distally. Basal endite bilobed; both distal and proximal lobes with 11 or 12 setae each. Coxal endite bilobed: distal lobe with seven setae; proximal lobe with 11 to 15 setae. Scaphognathite with 16 to 18 outer marginal setae, three apical setae and one on internal margin of posterior lobe (total 20 to 22 setae), all plumose. Fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with one or two distal setae. Basipodite with setae grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with three distal setae, inner margin; segment 2 with three distal setae, inner margin and one distal seta, outer margin; segment 3 with two medial and three distal setae, inner margin and one medial seta, outer margin; segment 4 with five or six terminal setae and one proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacks setae. Basipodite with three setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segments 1 and 2 each with two distal setae, inner margin and one distal, outer margin; segment 3 with one medial, two distal, inner margin and one medial seta, outer margin; segment 4 with four to six (usually five) terminal setae and one proximal seta on outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped III biramous, larger than in zoea I; endopodite curved anteriad; appendage grows and additional segments become defined during stage.

Pereiopods present as five pairs of limb buds, pairs one and five distinctly chelate; buds expand in size throughout stage and become distinctly segmented in a late zoea II.

Abdominal somites larger but otherwise similar to those in zoea I; pairs of pleopods, unequal in length, occur ventrally on segments 2, 3, 4, and 5; pleopods increase in length throughout stage.

Telson similar to form in zoea I but with single median seta (Figures 1E and 4I) added to central prominence and size increased; anal spine present.

Basic pattern of primary red chromatophores same as in prezoea and zoea I; however, new chromatophores appear in the late second stage zoea on the growing pereiopods and on body beneath carapace. Carapace 1.72 to 1.98 mm in length. Rostrum bears distinct ventral bulge just anterior to eyes (Figure 2E).

MEGALOPA
(Figures 5 and 6)

Antennule biramous with three-segmented peduncle. Dorsal ramus with six segments; segments 2, 3, and 4 each bear two tiers of aesthetascs and segment 5 bears one tier; numbers of aesthetascs per tier are approximately 3-4, 2-3, 3, 2, 2-3, 2, 2 progressing distally (specimens damaged); one long seta present on each of segments 3 and 4 associated with the distal aesthetasc tier. Ventral ramus with three distinct segments, the distal segment itself appearing indistinctly divided; setation as figured.

Antennal flagellum usually composed of 17 segments; peduncle three-segmented; hairs and bristles associated with the distal end of each segment along the length of the flagellum vary in number and pattern of distribution.

Mandible strongly sclerotized, partially cup-shaped appendage with bladelike leading edge which may be somewhat irregular but is not strongly toothed as in the zoea; three-segmented palp present with about six spinelike setae on terminal segment.

Maxilla I with probably two-segmented endopodite (specimens damaged) bearing one or more setae; basal endite with a total of 21 or 22 spines and setae arranged predominantly along the distal margin; coxal endite with approximately 26 processes, most of them slender setae in contrast to the spinelike processes of the basal

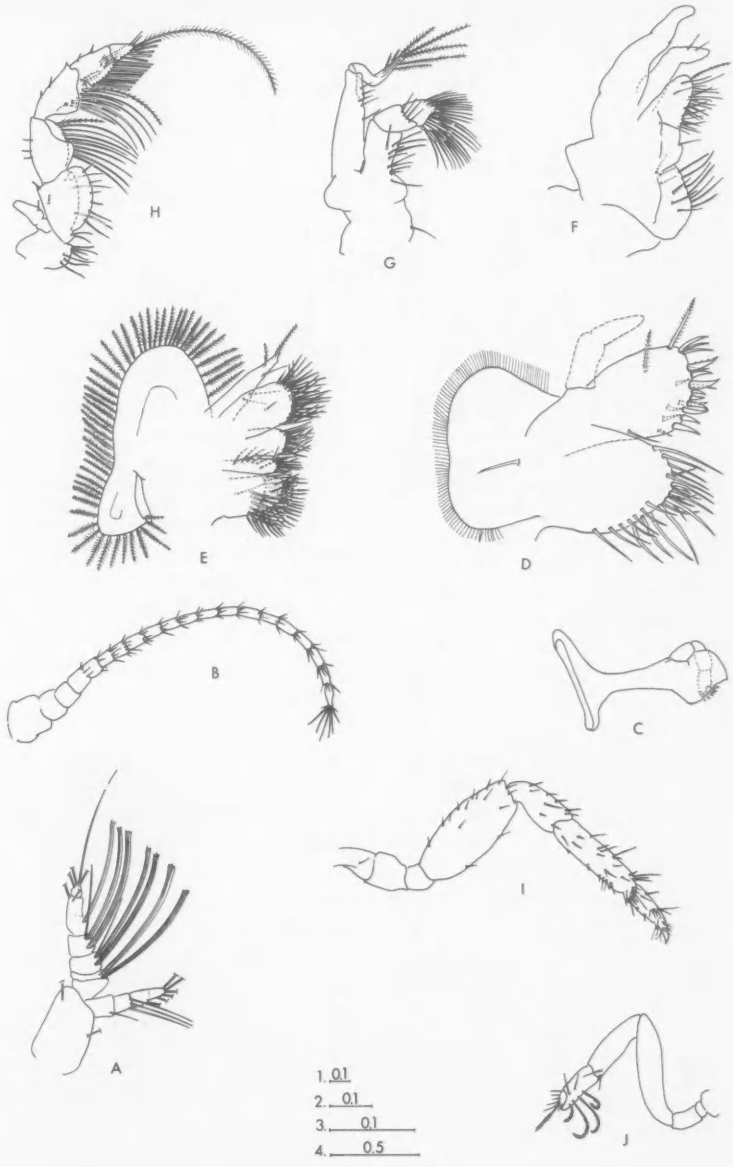

FIGURE 5.—*Petrolisthes cinctipes* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (B, G, H, J, Scale 1; A, C, E, F, Scale 2; D Scale 3; I, Scale 4). Scales in millimeter.

FIGURE 6.—*Petrolisthes cinctipes* and *P. eriomerus* megalopae: A - *P. cinctipes* megalopa, generalized, with chromatophore; B - *P. cinctipes* telson and uropods; C - *P. cinctipes* right third pleopod; D - *P. eriomerus* megalopa, generalized, with chromatophore; E - *P. eriomerus* telson and uropods; F - *P. eriomerus* right third pleopod (A, D, Scale 1; B, C, E and F, Scale 2). Scales in millimeter.

endite; a small fanlike exite also present, rimmed with very fine hairs.

Maxilla II with unsegmented endopodite bearing five setae. Basal endite bilobed: distal lobe with approximately 26 setae; proximal lobe with 13 to 15 setae. Coxal endite bilobed: distal lobe with nine marginal setae and six submarginal setae, dorsal surface; proximal lobe with about 20 marginal setae, 13 submarginals, dorsal surface, and 8 submarginal setae, ventral surface. Scaphognathite with approximately 50 marginal setae.

Maxilliped I biramous. Exopodite devoid of setae or hairs in specimens examined (two). Endopodite two-segmented in appearance, but indistinctly so; distal segment bears two short setae. Basal endite with 19 or 20 major marginal setae, 5 to 8 submarginal setae, dorsal surface. Coxal endite with about seven major marginal setae and six submarginal setae, three on dorsal surface and three on ventral surface.

Maxilliped II biramous. Exopodite consists of two distinct segments, the distal segment itself appearing indistinctly segmented; there are five to seven plumose setae on the distal segment and five setae on the internal margin of the first segment. Endopodite four-segmented, the distal two segments each bearing dense brushes of approximately 20 to 30 setae; segment 2 with four or five setae along distal margin; segment 1 with approximately 11 setae along the internal margin.

Maxilliped III biramous. Exopodite incompletely formed with two segments only; segment 2 with one small proximal seta. Endopodite specialized for filter feeding and consists of five segments; segment 2 with 10 to 12 major setae, dorsal internal margin; segment 3 with 9 or 10 major feeding setae, 3 or 4 short, stout brushlike setae, and 2 or 3 very short, spikelike setae all on the dorsal internal margin; segment 4 with nine major feeding setae along the internal ventral margin, six or seven minor feeding setae along dorsal internal margin; four or five major brush setae and two spikes, all along internal dorsal margin; segment 5 with six pairs of feeding setae and two minor brush setae terminally; other setation as pictured.

Pereiopods well developed and functional. Chelipeds slender and streamlined, generally dorsoventrally flattened with fine bristles over entire surface; outer margin of chelae produced in a series of spines; anterior margin of carpus with one major spine and a fine bristle associated with it. Pereiopods 2, 3, and 4 similar to each other in shape and setation as figured (Figure 5I). Pereiopod 5 chelate and armed with setae and bristles as shown; four to eight scythelike cleaning setae (Figure 1L, N) are also present.

Abdomen six-segmented; segments 2 through 5 each bearing one pair of pleopods. Pleopods biramous; exopodite with 16 plumose marginal setae; endopodite with two short setae and four hooks on margin. A single primary red chromatophore located on segment 2 or between 2 and 3. Segment 6 of the abdomen bears a pair of biramous uropods, the outer ramus usually having 14 and inner ramus with 15 marginal setae. Telson with 14 to 16 major plumose setae and 14 to 16 minor setae located between the major marginal setae. The dorsal surface of the telson bears a number of symmetrically placed pairs of fine hairs. In megalopae of advanced age, the beginning of the division of the telson into five plates can be seen beneath the cuticle. Upon molting to the first crab stage, the division of the telson is complete and distinct.

LARVAL DEVELOPMENT OF *PETROLISTHES ERIOMERUS* STIMPSON

Larvae of *P. eriomerus* were reared in unaerated Erlenmeyer flask cultures.

PREZOEA

The prezoea has essentially the same form as that described for *P. cinctipes* and differs only in one pair of primary chromatophores. *P. eriomerus* prezoeae lack the chromatophore on either side of the body between the bases of maxillipeds I and II which occurs in *P. cinctipes* larvae.

ZOEA I
(Figure 7)

Antennule unsegmented; five to six terminal processes including four aesthetascs and one or two setae.

Antenna biramous, with endopodite and protopodite fused; endopodite with terminal point, subterminal tubercle and fine seta between; exopodite approximately 1⅓ times as long as endopodite with one, two, or three prominent distal spines and one long seta proximal to spines.

Mandibles strongly sclerotized asymmetrical appendages, heavily armed with teeth and tubercles on leading edges.

Maxilla I with unsegmented endopodite bearing three to six terminal and subterminal setae and a number of fine hairs along anterior margin; basal endite with 9 or 10 setae; coxal endite with 8 to 10 setae.

Maxilla II with unsegmented endopodite which bears 7 to 10 setae, grouped 2-3, 2, 3-4 progressing distally. Basal endite bilobed: distal lobe with 8 to 10 setae; proximal lobe with 6 to 10 setae. Coxal endite bilobed: distal lobe with four to eight setae; proximal lobe with 7 to 11 setae. Scaphognathite with six to eight long plumose marginal setae and one strong apical seta. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with two or rarely three distal setae. Basipodite with 10 setae usually grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three distal setae, inner margin; segment 3 with usually two medial and three or rarely four distal setae, inner margin; segment 4 with five to seven terminal setae and one proximal seta, outer margin; segments 2 and 3 also bear groups of fine hairs as figured. Exopodite two-segmented, the distal segment bearing four terminal natatory setae.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with usually two but sometimes one distal seta and one medial seta, inner margin. Endopodite four-segmented: segment 1 with usually two but sometimes with one distal seta, inner margin; segment 2 usually with two but rarely one or three distal setae, inner margin; segment 3 with one medial seta or occasionally two setae, and usually two, but sometimes three distal setae, inner margin; segment 4 with three to five terminal setae and one proximal seta, outer margin; segments 2 and 3 also bear groups of fine hairs as figured. Exopodite two-segmented, the distal segment bearing four terminal natatory setae.

Maxilliped III a small bilobed bud which grows throughout stage.

Pereiopod buds simple, five pairs in number, growing throughout the duration of the stage.

Abdominal segments five in number; segments 3, 4, and 5 having serrations on dorsal posterior margins; segments 4 and 5 with strong ventrolateral spines on posterior margin.

Telson with seven symmetrically placed pairs of processes, with seventh pair on central prominence. Outer margin to center line: one heavy lateral spine fused with telson, one short fine seta, and five long plumose articulating setae, all armed distally with a series of short, curved fixed spines (Figure 1D); numerous fine hairs on telson margin (not figured) between all major plumose setae; anal spine present.

Chromatophore pattern as noted for the prezoea; extended rostrum with one terminal and one subterminal band of red color; posterior spines each with one terminal red band. Carapace 1.31 to 1.48 mm in length.

ZOEA II
(Figure 8)

Antennule biramous; exopodite with six or seven terminal processes including four aesthetascs and two or three setae followed by five tiers of subterminal aesthetascs grouped 3, 4, 3, 3, 2 proximal to distal.

Antenna biramous; endopodite same form as in zoea I; exopodite similar to that in zoea I with one to three spines, one seta distally; spines somewhat less prominent than in zoea I; exopodite approximately three-quarters length of endopodite.

Mandibles larger than in zoea I and with prominent palp bud.

FIGURE 7.—*Petrolisthes eriomerus* zoea I: A - antennule; B - antenna; C - mandibles; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and periopod buds; I - abdomen and telson (A-E, H, Scale 2; F, G, I, Scale 1). Scales in millimeter.

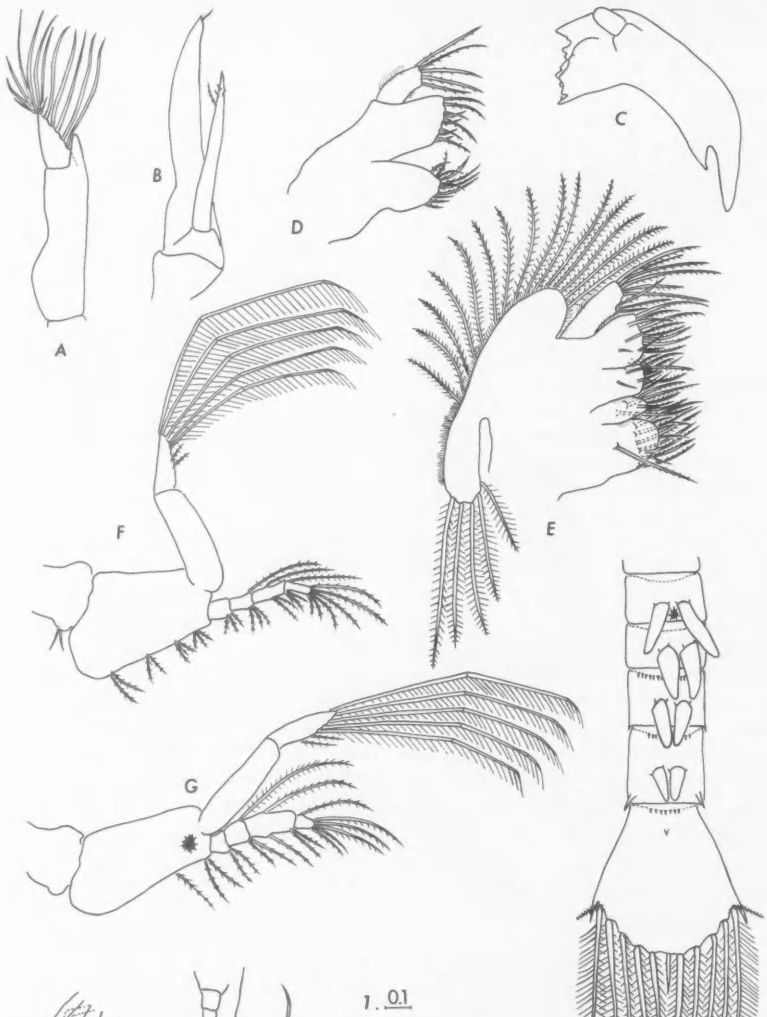

FIGURE 8.—*Petrolisthes eviomerus* zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopods; I - maxilliped III, late zoea II; J - abdomen and telson (A, B, F-H, J, Scale 1; C-E, I, Scale 2). Scales in millimeter.

Maxilla I with unsegmented endopodite bearing four to seven terminal and subterminal setae and a group of fine hairs along anterior margin; basal endite with 10 or 11 setae; coxal endite with 9 to 11 setae.

Maxilla II with unsegmented endopodite bearing nine setae grouped 3, 2, 4 progressing distally. Basal endite bilobed: distal lobe with 12 or 13 setae; proximal lobe with 11 or 12 setae. Coxal endite bilobed: distal lobe with five to seven setae; proximal lobe with 12 to 15 setae. Scaphognathite with 13 to 16 marginal, 3 apical, and 1 or 2 internal lateral setae (total 17 to 21); fine hairs present on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with two distal setae. Basipodite with setae usually grouped 2, 2, 3, 3 proximal to distal along inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three or four distal setae, inner margin and one distal seta, outer margin; segment 3 usually with two medial and three distal setae, inner margin and one medial, outer margin; segment 4 with four to seven terminal and one proximal seta, outer margin. Exopodite two-segmented, the distal segment bearing 14 natatory setae.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with three distal setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with two (occasionally one) distal setae, inner margin; segment 2 with two distal setae, inner margin and one distal setae, outer margin; segment 3 with one medial, two or rarely three distal, inner margin, and one medial seta, outer margin; segment 4 with five terminal setae and one proximal seta, outer margin. Exopodite with two segments, the distal segment bearing 14 natatory setae.

Maxilliped III biramous. Exopodite indistinctly divided with two segments; zero to three setae have been observed on endopodite. Endopodite with up to five segments apparent beneath cuticle, depending on the age of the zoea.

Pereiopod buds five pairs in number with first and fifth pairs distinctly chelate; buds increase in length throughout the stage.

Abdominal somites numbering five, similar to form in zoea I but larger and with paired pleopod buds of unequal length on segments 2 through 5; pleopods increase in length throughout the stage.

Telson similar to form in zoea I but larger and with one unpaired median seta on the central prominence (Figures 1E and 8J).

Pattern of primary chromatophores same as that in zoea I but new ones may be added on the growing pereiopods. Carapace 1.80 to 1.89 mm in length. Rostrum bears distinct ventral bulge just anterior to eyes.

MEGALOPA
(Figures 6 and 9)

Antennule biramous with three-segmented peduncle. Dorsal antennular ramus six-segmented; segments 2, 3, 4, and 5 with 2, 2, 2, 1 tiers of aesthetascs respectively; tiers, progressing distally, contain approximately 6-7, 6-7, 6-7, 3-4, 3, 2, 3 aesthetascs respectively; one long slender seta associated with the distal tier on each of segments 3 and 4. Ventral ramus with three segments; setation as figured.

Antenna long and slender with three-segmented peduncle; flagellum with 28 to 30 segments; most segments armed distally with variable numbers of short bristles and hairs as figured.

Mandible differs from toothed form in zoeal stages and is partially cup-shaped with slightly irregular bladelike leading edge; three-segmented palp has seven to ten spines on distal segment.

Maxilla I with indistinctly two-segmented endopodite bearing a single terminal seta on the distal segment and a single seta situated at base; basal endite with a total of about 25 stout spines and setae; coxal endite with a total of 32 stout setae. In addition, there is a single long seta proximally on the exopodite and a delicate exite edged with fine hairs associated with coxal portion of appendage.

Maxilla II with slender, indistinctly segmented endopodite bearing three terminal setae and one

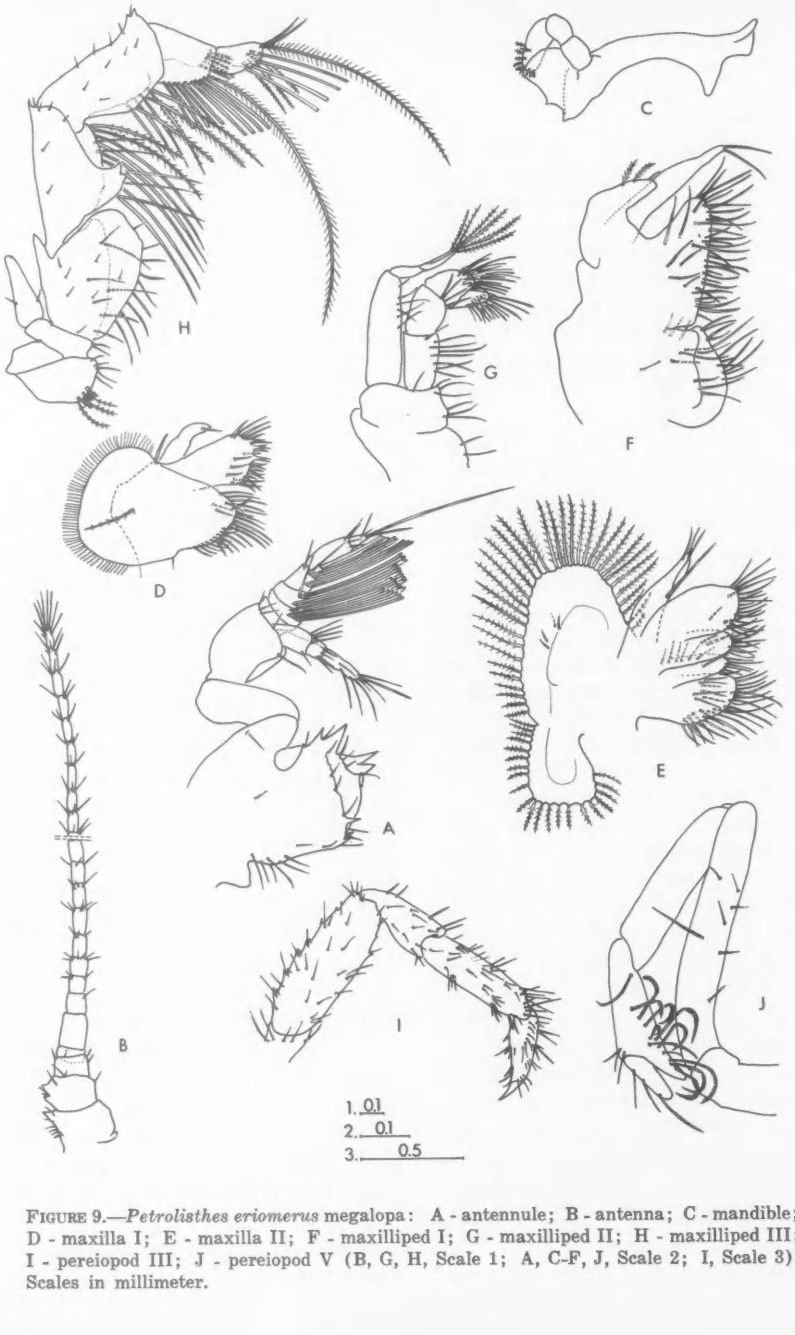

FIGURE 9.—*Petrolisthes eriomerus* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (B, G, H, Scale 1; A, C-F, J, Scale 2; I, Scale 3). Scales in millimeter.

lateral seta. Basal endite bilobed: distal lobe with 32 to 34 setae; proximal lobe with about 19 setae. Coxal endite bilobed: distal lobe with about 19 setae; proximal lobe with about 39 setae.

Maxilliped I with exopodite bearing three marginal setae; endopodite with two terminal setae in specimens dissected; basal portion of protopodite produced into triangular lobe bearing 35 to 42 setae; coxal lobe with numerous setae numbering 16 to 21 in specimens counted.

Maxilliped II with two-segmented exopodite usually bearing six setae on terminal segment and six internal marginal setae on proximal segment. Endopodite composed of four segments the distal two of which are armed with dense setal brushes each containing about 16 to 20 setae. Other setation as figured.

Maxilliped III with single-segmented exopodite bearing two very fine setae. Endopodite with five well-developed segments; segments 2 through 5 armed with filtering setae; segment 2 with 13 major setae along dorsal inner margin; segment 3 with three major ventral and four or five major dorsal internal marginal feeding setae, seven or eight minor submarginal brushlike setae dorsally and five ventral major submarginal brush setae; segment 4 with 10 major ventral marginal feeding setae, 9 minor dorsal marginal feeding setae, protuberance distally and dorsally on segment bearing a row of 5 major brush setae and a subordinate row of 4 spikelike setae and 1 fine seta; segment 5 with five major ventral and four or five dorsal (mixed major and minor) feeding setae, two slender terminal brush setae; three major brushes and two spikes on dorsal, submarginal bulge.

Pereiopods well developed and functional. Chelae slender, narrow, dorsoventrally flattened with two fixed spines present on internal margin of carpus. Walking legs all similar in form and setation as figured. Pereiopod 5 chelate with bristles and hooked setae for cleaning as figured.

Abdomen segments numbering 6, segments 2 through 5 with paired biramous pleopods; marginal setation of pleopod exopodites varies from 10 to 13, the higher numbers generally being found on the more proximal pleopods; each pleopod endopodite is armed with four small hooks and two setae. Segment 2 bears one chromatophore distally. A pair of biramous uropods articulate with segment 6; the outer ramus with 15 or 16 marginal setae, inner ramus with 10 or 11 marginal setae.

Telson with 15 or 16 major marginal plumose setae and usually four minor setae placed approximately symmetrically with respect to the center line of the telson between the major marginal setae; dorsal surface of telson bears about 10 pairs of fine setae in approximately symmetrical positions.

LARVAL DEVELOPMENT OF *PACHYCHELES PUBESCENS* HOLMES

Larvae taken from the plankton were reared in unaerated Erlenmeyer flask cultures and identified at a later date by comparison with laboratory hatched larvae.

PREZOEA

The general body form of *Pachycheles pubescens* is the same as that described for *Petrolisthes cinctipes* prezoeae; however, certain details of the prezoeal cuticle of the telson differ from *P. cinctipes*. The prezoeal cuticle of *Pachycheles pubescens* is produced into flat spines with toothed margins (Figure 2), an additional adaptation for swimming by abdominal flexion. Chromatophores occur as follows: one on either side of the mouth; one each on abdominal segments 1, 2, 3, and 5; and one on the telson.

ZOEA I
(Figure 10)

Antennule unsegmented with five or six terminal processes including three or four aesthetascs and one or two setae.

Antenna biramous with endopodite and protopodite fused; endopodite without subterminal tubercle or fine seta; exopodite 1¾ to 2 times as long as endopodite; usually three short stout, curved spines along internal lateral margin distally on exopodite, but spines occasionally number one or two and rarely four.

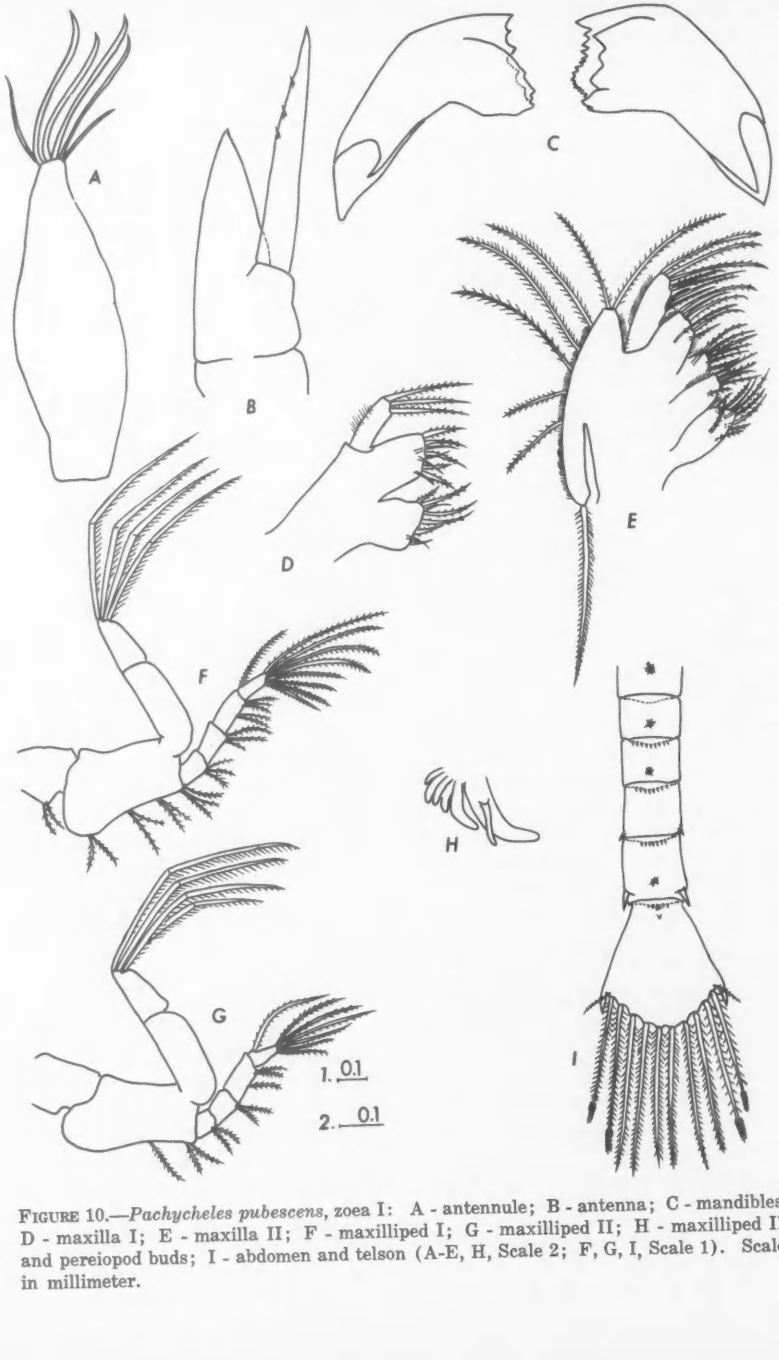

FIGURE 10.—*Pachycheles pubescens*, zoea I: A - antennule; B - antenna; C - mandibles; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopod buds; I - abdomen and telson (A-E, H, Scale 2; F, G, I, Scale 1). Scales in millimeter.

Mandibles strongly toothed, heavily sclerotized asymmetrical appendages.

Maxilla I with unsegmented endopodite bearing three to five terminal setae and a number of fine hairs along anterior margin; basal endite with eight or nine setae; coxal endite with seven to nine setae.

Maxilla II with unsegmented endopodite bearing eight or nine setae grouped 3, 2, 3-4 progressing distally. Basal endite bilobed: distal lobe with six to eight setae; proximal lobe with six to eight setae. Coxal endite bilobed: distal lobe with three to five setae; proximal lobe with six to nine setae. Scaphognathite with seven long plumose marginal setae and one apical seta on posterior lobe. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite usually with two distal setae. Basipodite usually with nine setae arranged 2, 2, 2, 3 proximal to distal along inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three distal setae, inner margin; segment 3 usually with one, sometimes two medial setae, and usually three, sometimes two or four distal setae, inner margin; segment 4 with seven to nine terminal setae and one long proximal seta, outer margin. Exopodite two-segmented with four natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with one medial, two distal setae, inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with two distal setae, inner margin; segment 3 with one medial and one or two distal setae, inner margin; segment 4 with five or six terminal and one proximal seta, outer margin. Exopodite two-segmented with four terminal natatory setae.

Maxilliped III present as small bilobed bud which increases in size during the stage.

Pereiopod buds numbering five pairs, simple; none chelate; buds increase in size throughout stage.

Abdominal somites five in number; segments 4 and 5 with prominent paired ventrolateral spines on posterior margin; segments 2 through 5 with serrated dorsal posterior margins.

Telson with seven symmetrically arranged pairs of processes with seventh pair on central prominence. Outer margin to center line: one heavy lateral spine fused with telson; one short, fine seta; five long plumose articulating setae, the outer two armed distally with fixed, curved spines (Figure 1A, B); fine hairs on margin of telson (not figured) between all major plumose setae and on central prominence.

Chromatophore pattern same as that described for prezoea. Rostrum commonly with three bands of red, one terminal and two subterminal, occasionally with only one subterminal band; both posterior spines tipped with red. Carapace 1.31 to 1.56 mm long.

ZOEA II
(Figure 11)

Antennule biramous; exopodite with six or seven terminal processes including three or four aesthetascs and two or three setae followed by five tiers of aesthetascs grouped 2, 3, 3, 4-5, 4-6 proceeding proximally. One long seta projects from distal portion of protopodite.

Antenna biramous; endopodite pointed terminally and armed subterminally with one fine seta and two small spines; exopodite unarmed and about two-thirds length of endopodite.

Mandibles increased in size; prominent palp bud present.

Maxilla I with unsegmented endopodite bearing three or four terminal setae and a group of fine hairs along anterior margin; basal endite with 9 or 10 heavy spinous setae; coxal endite with 8 to 11 heavy spinous setae.

Maxilla II with unsegmented endopodite bearing nine setae. Basal endite bilobed: distal and proximal lobes each with 9 to 11 setae. Coxal endite bilobed: distal lobe with four to seven setae; proximal lobe with 10 to 13 setae. Scaphognathite with 18 setae on outer margin and 3 strong apical setae on posterior lobe. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

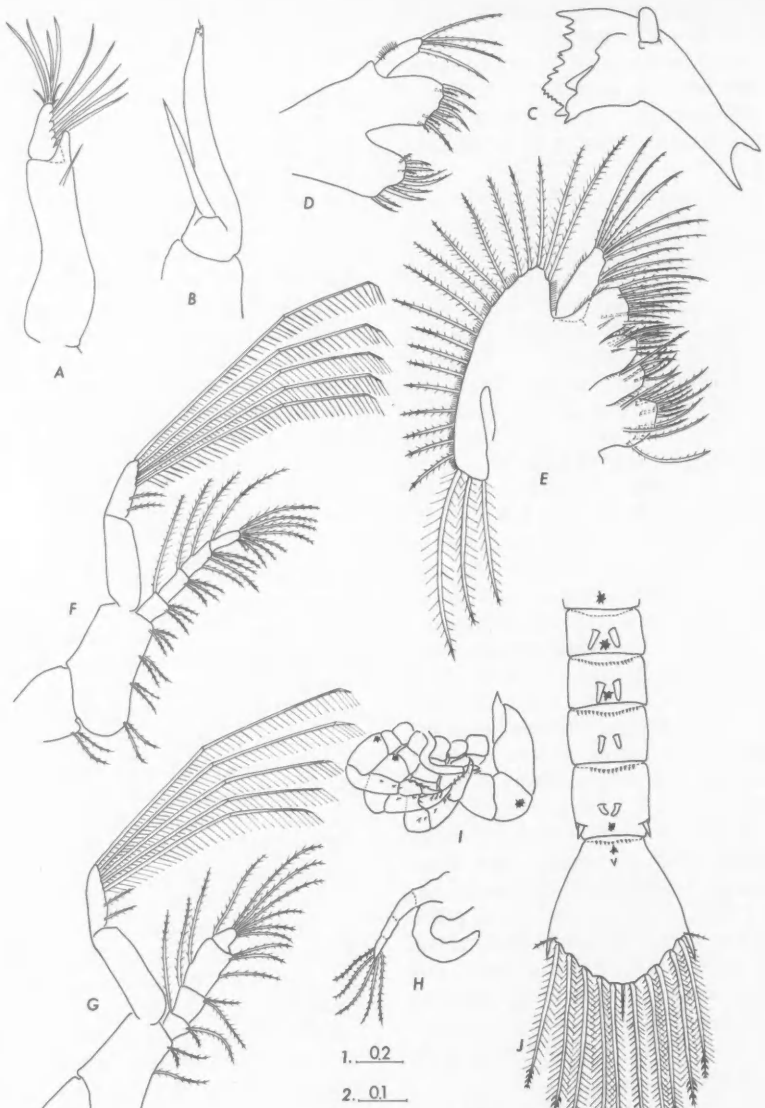

FIGURE 11.—*Pachycheles pubescens*, zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III, late zoea II; I - pereiopods; J - abdomen and telson, early zoea II (A, B, F-J, Scale 1; C-E, Scale 2). Scales in millimeter.

Maxilliped I biramous. Coxopodite usually with two distal setae. Basipodite usually with nine setae along inner margin grouped 2, 2, 2, 3 proximal to distal. Endopodite four-segmented: segments 1 and 2 each usually with three distal setae (segment 2 occasionally with four), inner margin and one distal seta, outer margin; segment 3 most commonly with one but occasionally two medial, two to four distal setae, inner margin and one medial seta, outer margin; segment 4 with 8 to 11 terminals and 1 proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite usually with three setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin and one distal seta, outer margin; segment 2 with one or two distal setae, inner margin and one distal seta, outer margin; segment 3 usually with one (occasionally none) medial, two distal setae, inner margin, and one medial seta, outer margin; segment 4 with five terminals and one proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped III a bilobed bud. Exopodite increases in size throughout stage; four to six setae present; one or two definite segments present beneath cuticle, depending on age of zoea. Endopodite entire or segmented with up to five segments beneath cuticle, depending on age; setae of megalopa stage visible beneath cuticle of advanced zoea.

Pereiopod buds enlarge during stage and become well developed; first and fifth pairs distinctly chelate. Spines and claws appear on pereiopods in advanced, premolt larva.

Abdominal somites larger than in zoea I but similar in form; segments 2, 3, 4, and 5 each bear a pair of pleopods of unequal length.

Telson increased in size; an unpaired median seta added on central prominence (Figures 1C and 11J); anal spine present.

Basic color pattern same as in zoea I; red chromatophores added to pereiopods and beneath carapace in zoeae of advanced age. Carapace 2.37 to 2.54 mm in length.

MEGALOPA
(Figures 12 and 13)

Antennule biramous, consisting of a three-segmented peduncle, a dorsal ramus with six segments, and a ventral ramus with three segments. Segments 2, 3, and 4 of dorsal ramus each bear two tiers of aesthetascs; segment 5 with only 1 aesthetasc tier. Numbers of aesthetascs per tier proximal to distal 7-8, 8, 6-7, 5, 4, 2, 3. One long seta associated with distal tier of aesthetascs on segments 2, 3, and 4. Other setation as figured.

Antennal flagellum composed of 29 to 30 segments in addition to the three-segmented peduncle; most segments bear variable numbers of fine bristles around the distal margin as figured.

Mandible highly sclerotized with three-segmented palp; terminal segment of palp with about 17 spines; grinding edge only slightly irregular with a generally bladelike form.

Maxilla I with a two-segmented endopodite bearing a single distal seta on terminal segment. Basal endite with 7 slender setae and 14 heavy spinelike setae along distal margin; also seven short, stout, spinelike setae submarginally on dorsal surface of segment. Coxal endite with four setae on dorsal surface and about 29 marginal and near submarginal setae; delicate fanlike coxal exite rimmed with hairs is present.

Maxilla II with unsegmented endopodite which bears five or six setae. Basal endite bilobed: distal lobe with 33 to 36 setae; proximal lobe with about 22 setae. Coxal endite bilobed: distal lobe with about 20 setae; proximal lobe with about 38 setae. Scaphognathite with about 68 marginal plumose setae and 5 short fine hairs on the surface of the fan.

Maxilliped I with exopodite bearing nine setae. Endopodite indistinctly two-segmented, bearing one seta on distal segment. Protopodite with about 52 setae. Coxal endite with about 23 setae.

Maxilliped II biramous; exopodite indistinctly two-segmented with eight or nine terminal setae; endopodite four-segmented, segments 3 and 4 having heavy terminal brushes of about 26 and 30 setae respectively; other setation as figured.

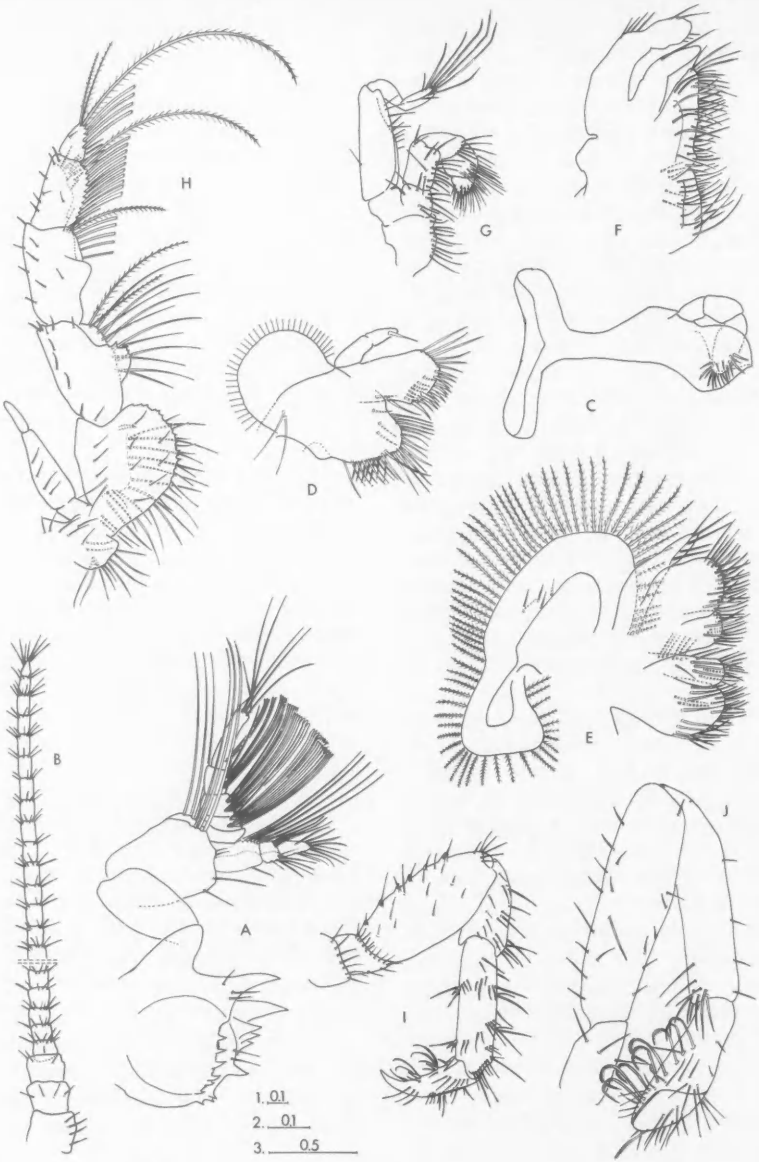

FIGURE 12.—*Pachycheles pubescens*, megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (A, C-F, J, Scale 2; B, G, H, Scale 1; I, Scale 3). Scales in millimeter.

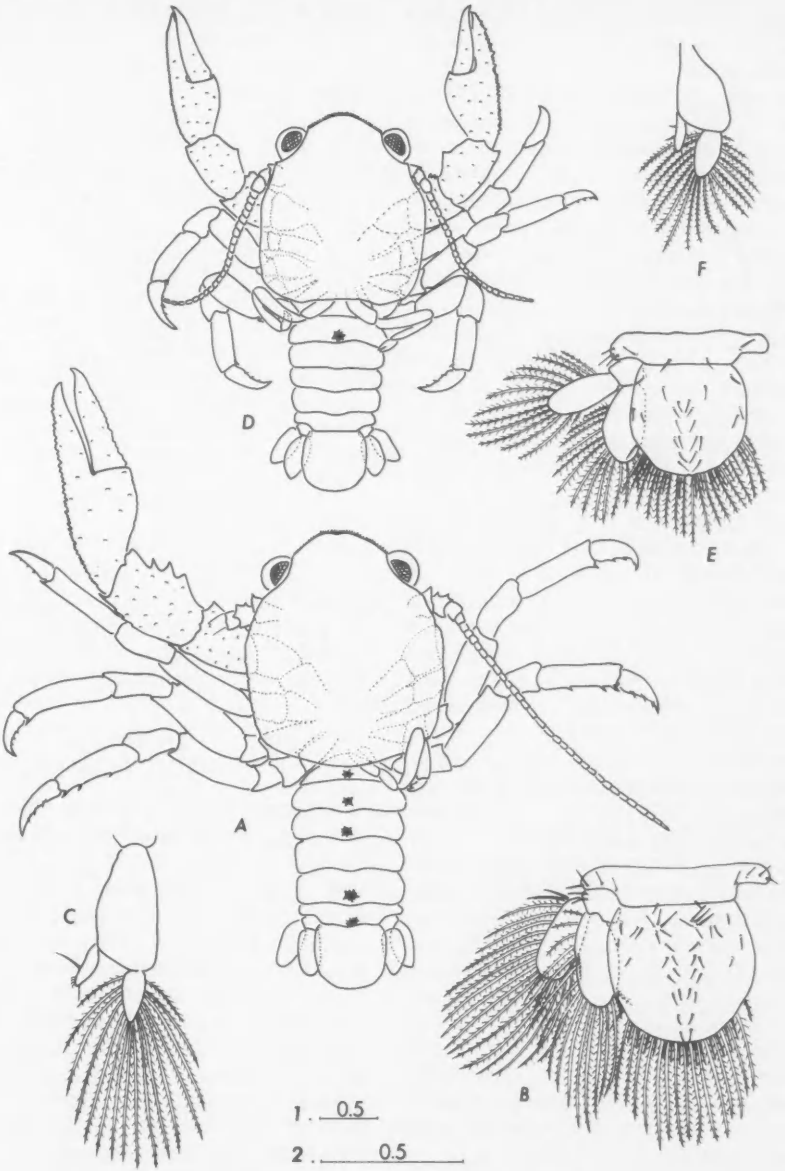

FIGURE 13.—*Pachycheles pubescens* (A-C) and *P. rudis* (D-F) megalopae, whole mounts: A - *P. pubescens* megalopa, whole mount; B - telson and uropods; C - right third pleopod; D - *P. rudis* megalopa, whole mount; E - telson and uropods; F - right third pleopod (A, D, Scale 1; B, C, E, F, Scale 2). Scales in millimeter.

Maxilliped III biramous; exopodite two-segmented, terminal segment being incomplete and lacking setae. Endopodite with five segments; segment 2 with 13 major marginal setae in double row (7, 6); segment 3 with five or six slender minor setae, outer margin, six major inner marginals, and nine brush setae, inner margin; segment 4 with five major and three spike-like brush setae, inner margin, 11 outer major marginals, and 7 inner minor auxiliaries; segment 5 with five pairs of major feeding setae, one or two pairs of minor terminal setae.

Pereiopods well developed and functional. Chelipeds large, swollen and bristly; two or three prominent fixed spines on the anterior margin of carpus. Three pairs of walking legs similar in form and setation as figured. Pereiopod 5 with 8 to 10 sickle-shaped setae and a number of other bristles.

Abdominal segments six in number, segments 2 through 5 with paired biramous pleopods bearing setae as follows: 16 marginal setae on exopodite; endopodite armed with four small hooks and two setae. Chromatophores appear posteriorly in segments 1, 2, 3, 5, and 6. Segment 6 bears a pair of biramous uropods, the outer rami each with about 19 plumose marginal setae and the inner with 17 or 18 such setae.

The telson has 15 or 16 major marginal setae. Minor marginal setae are present between almost all major setae. The dorsal surface of the telson is equipped with a number of very fine short hairs arranged in approximate symmetry as figured. Frontal margin of carapace as figured (Figure 13A).

LARVAL DEVELOPMENT OF *PACHYCHELES RUDIS* STIMPSON

In the laboratory, only a single *P. rudis* larva reared at 15°C and 33‰ salinity reached the megalopa stage. Laboratory-reared material was extensively supplemented with larvae from the plankton for purposes of examination.

Knight (1966) has dissected and accurately described the two true zoeal stages of *P. rudis*. She also adequately described the gross external morphology of the megalopa stage. Owing to high mortality in her cultures, she was forced to describe the larvae of this species on the basis of very few specimens. In this study, numbers of laboratory-hatched larvae surviving each stage in cultures were comparable to numbers obtained by Knight (1966), but the various stages were extremely abundant in the plankton. Knight's description of the species is expanded here using this more plentiful material.

PREZOEA

Body form is the same as that described for *Petrolisthes cinctipes* (Figure 2). Chromatophores occur as follows: one on either side of the mouth; one posteriorly in abdominal segment 2 or between segments 2 and 3. This is the least colorful of the species discussed here. Knight (1966) does not mention a prezoeal stage.

ZOEA I AND II

Table 2 indicates points in which the larvae studied here differ from those described by Knight (1966). Differences are minor but are included to establish a more accurate range of variability for this species.

MEGALOPA
(Figures 13 and 14)

Antennule biramous with three-segmented peduncle. Dorsal ramus with six segments, segments 2 through 5 bearing 2, 2, 2, and 1 tier of aesthetascs respectively. Aesthetascs are arranged 6, 6-7, 5-6, 3-4, 3-4, 2, 3 in tiers progressing distally. A single long plumose seta is associated with the distal tier on segments 2, 3, and 4. Ventral ramus distinctly three-segmented, the most distal segment being indistinctly divided. Other setation and spination as figured.

Antenna long, slender, with three-segmented peduncle; flagellum with 20 to 21 segments; variable numbers of fine hairs and bristles arranged distally on most segments as figured.

Mandible strongly sclerotized, partially cup-shaped appendage with three-segmented palp; distal segment of palp with about 13 terminal spines as figured.

TABLE 2.—Comparison of species descriptions of *Pachycheles rudis*.

Stage	Appendage	Knight (1966)	This study
Zoea I	Antennule	6 processes including 3 aesthetascs, 2 setae	6-7 processes including 4 aesthetascs, 1-2 setae
Zoea II	Antennule	7 processes, including 3 aesthetascs, 2 setae	6-7 processes including 4 aesthetascs, 2-3 setae
Zoea II	Maxilla I: Coxal endite	5 spines, 6 setae	10 setae
Zoea II	Maxilla II:		
	Basal endite, distal lobe	10-12 setae	11-12 setae
	Basal endite, proximal lobe	10 setae	10-11 setae
	Coxal endite, distal lobe	6 setae	6- 7 setae
	Coxal endite, proximal lobe	10-12 setae	9-10 setae
Zoea II	Maxilliped I:		
	Basipodite	Setae grouped 2, 2, 3, 3	Setae grouped 2, 2, 2, 3
	Endopodite, segment 3	2 medial setae	1-2 medial setae
	Endopodite, segment 3	3 distal setae	3-4 distal setae[1]
	Endopodite, segment 4	7-8 terminal setae[1]	8-9 terminal setae[1]
Zoea II	Maxilliped II: Endopodite, segment 1	2 distal setae, inner margin	2-3 distal setae, inner margin
Zoea II	Maxilliped III: Exopodite	2 slender setae	2 slender setae, and 2-3 fine setae
All larval stages	Abdominal segment 2 or between 2 and 3	--	1 chromatophore
	Either side of mouth	--	1 chromatophore

[1] Most common occurrence in bold face.

Maxilla I with indistinctly two-segmented endopodite bearing two stout setae on distal segment. Basal endite with 8 long, slender and 16 stout, spinous setae on margin and 6 short setae on ventral surface. Coxal endite with about 26 marginal setae and 4 fine setae on ventral surface. Coxal exite present as delicate fleshy lobe rimmed with fine hairs. One proximal seta on appendage near articulation with gnathal skeleton.

Maxilla II with large numbers of setae. Endopodite unsegmented with five setae. Basal endite bilobed: distal lobe with about 35 setae; proximal lobe with 9 or 10 marginal and 4 submarginal setae. Coxal endite bilobed: distal lobe with 20 to 21 setae arranged as figured; proximal lobe with 30 to 35 setae arranged as figured. Scaphognathite with about 58 setae around the margin and 2 fine submarginal setae on the anterior lobe.

Maxilliped I with numerous setae. Exopodite fleshy with one seta on margin. Endopodite indistinctly two-segmented, bearing a single seta proximally. Protopodite produced into triangular lobe with about 35 to 45 marginal setae and 3 proximal setae as figured. Coxal lobe with a total of about 18 setae arranged as figured.

Maxilliped II biramous. Setation of coxopodite and basipodite variable, approximately as figured. Exopodite two-segmented with setae as figured, with eight or nine setae on terminal segment. Endopodite with four segments; segments 3 and 4 having distal brushes of short setae numbering about 24 to 28 and 16 to 20 respectively. Other setation as figured.

Maxilliped III biramous. Exopodite two-segmented but incompletely formed. Segments 2 through 5 of endopodite equipped with major feeding setae; segment 2 with 11 or 12 feeding setae of two lengths, dorsal margin; segment 3 with five or six feeding setae on ventral margin, seven feeding setae or dorsal margin, and seven brush setae of varying lengths; no spikelike setae on dorsal protuberance; segment 4 with 2 short setae, 5 major brushes and 4 spike setae on dorsal protuberance, 10 long feeding setae on ventral margin, and 9 scattered minor submarginal setae on ventral surface; segment 5 with 10 or 11 marginal setae and 2 or 3 short terminal setae. Other setation as figured.

Details of setation and form of the walking

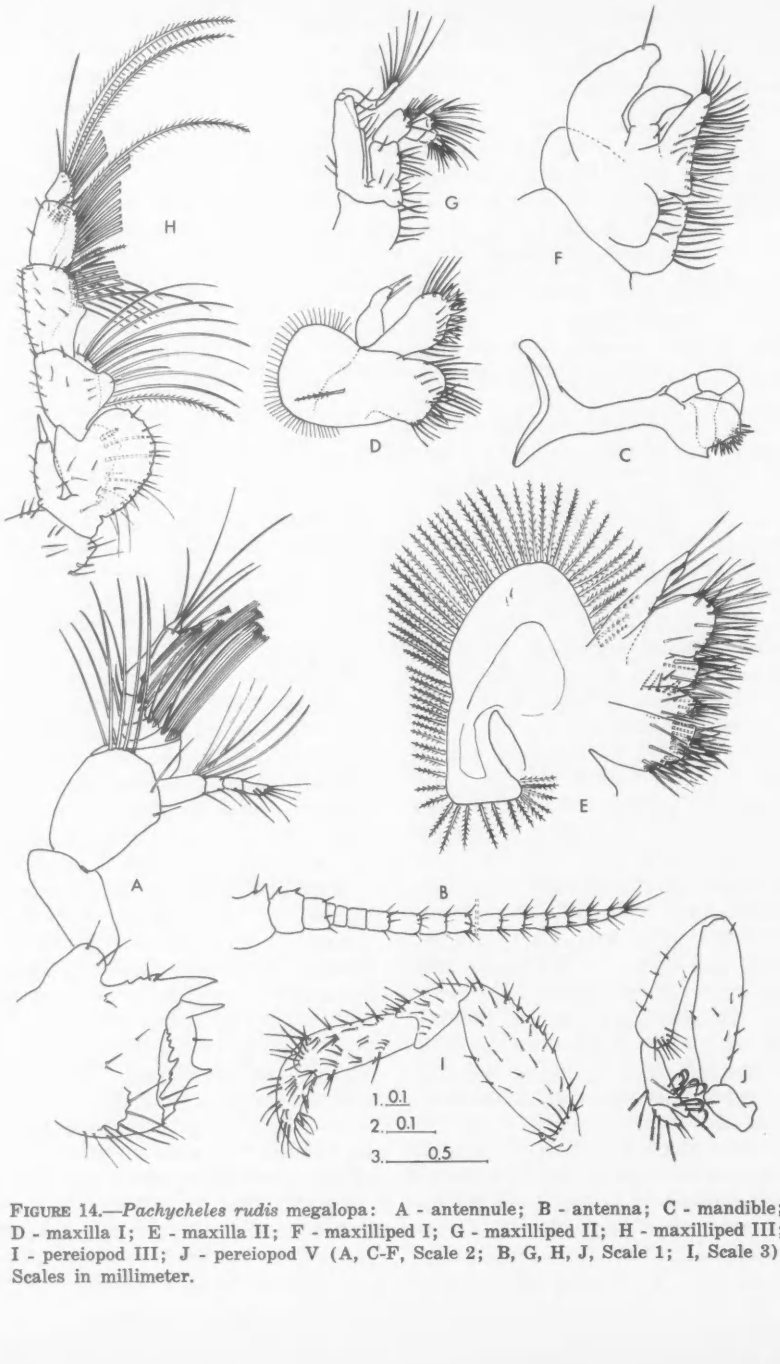

FIGURE 14.—*Pachycheles rudis* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (A, C-F, Scale 2; B, G, H, J, Scale 1; I, Scale 3). Scales in millimeter.

legs, the fifth pereiopods, the telson and sixth segment, and the frontal margin of the carapace are as figured.

DISCUSSION

The four species whose larvae are described here are the only porcellanids known (Haig, 1960) on the Pacific coast of North America north of Bodega Head, Calif., and we have found their larvae simultaneously in the plankton off the central Oregon coast. Both preserved and live zoea larvae of these four species can be readily assigned to genus on the basis of the number of long telson setae bearing conspicuous distal spines and the nature of these spines (Table 3). Once live or freshly killed zoeae are separated by genus using telson characters, individuals of the congeneric species can be separated to species on the basis of the distribution of the primary red chromatophores. Zoea larvae from preserved plankton samples cannot be identified to species easily once the chromatophores have faded. The only other nonvariable character found which distinguishes the species was maxillipedal setal counts, and it is possible that further study will indicate that these counts are also variable.

The two *Pachycheles* species differ in both zoeal stages by a single seta on the inner margin of segment two of the endopodite on maxilliped I (Table 4). In addition, second zoea larvae of these two species differ by a single seta on the outer margin of endopodite segment 1 on maxillipeds I and II (Table 4). Similar characters separate the larvae of the two *Petrolisthes* species. First zoeae differ by one seta on the inner margin of segment two of the endopodite of both maxillipeds I and II (Table 5). Second zoeae of these *Petrolisthes* differ by a single seta on the outer margin of the first segment of the endopodite on maxilliped II (Table 5). Megalopae of all four species can be readily differentiated on the basis of cheliped form and other finer characters (Figures 12-14).

Available knowledge of the larvae of *Pachycheles* species does not support Haig (1960) who, studying adult animals, suggested that *P. rudis* is most closely related to *P. stevensii*. A comprehensive comparison (Table 4) of the four most similar larvae of the *Pachycheles* species studied thus far does not definitely indicate such a relationship. On the basis of larval form and setal numbers, all four of the species are equally similar.

At this time too few porcellanid larvae have been described to use larval characters to draw firm conclusions about generic and specific relationships. There is however a need for means to identify as closely as possible porcellanid zoea larvae taken from the plankton in regions where larvae of all of the porcellanid species have not been reared. For all known porcellanid larvae of established specific identity, we have listed in Table 3 three morphological characteristics which appear to assign porcellanid zoeae to genera or generic groups. The following discussion evaluates the usefulness of these characteristics in grouping presently known larvae systematically. Planktonic larvae of uncertain adult origin are included and grouped with known larvae they most closely resemble, but are not discussed further. Two New Zealand porcellanids for which larvae have been described, *Petrolisthes novaezelandiae* and *P. elongatus*, have some unusual characteristics in both the larval and adult forms which distinguish them from all other porcellanids known. For this evaluation, they are conditionally placed with groups with which they share the larval characters listed in Table 3.

All presently known porcellanid zoeae can be placed in one of three groups on the basis of telson form. Lebour (1943) originally established two of these groups (A and B, Table 3) by distinguishing larvae of the genus *Porcellana* from larvae of the genus *Petrolisthes* as the genera were known at that time. Lebour's original *Petrolisthes* type telson group (B, Table 3) now includes all described species of the genera *Pachycheles* and *Megalobrachium* and all but one of the described *Petrolisthes* larvae, *P. novaezelandiae*. Wear (1964a) has suggested that the exceptional *P. novaezelandiae* be placed in the genus *Pisidia* on the basis of both larval and adult characters. Lebour's original *Porcellana* type telson group (A, Table 3) now includes all described larvae of the genera *Euceramus, Poly-*

TABLE 3.—Comparison of porcellanid larvae on the basis of distal armature of telson processes and telson form.[1]

Species	Position of armed telson processes		Type of armature on setae	Telson form	Author
	Zoea I	Zoea II			
Pachycheles rudis	3,4	3,4	All *Pachycheles* spp. have equal number of spines on inner and outer margins.	B	Knight, 1966
Pachycheles pubescens	3,4	3,4		B	This study
Pachycheles stevensii	3,4	3,4		B	Kurata, 1964
Pachycheles haigae	3,4	3,4		B	Boschi et al., 1967
Pachycheles natalensis	3-7	?	Spines most prominent on 5th process.	B	Sankolli, 1967
Megalobrachium poeyi	0	0		B	Gore, 1971
Petrolisthes cinctipes	3-7	3-7	Spines, equal number inner and outer margins (first 5 species listed).	B	This study
Petrolisthes eriomerus	3-7	3-7		B	This study
Petrolisthes armatus	3-7	3-7		B	Lebour, 1943, 1950 Gurney, 1938 Gore, 1970, 1972
Petrolisthes lamarckii	3-7	?	Spines most prominent on 5th process.	B	Sankolli, 1967
Petrolisthes boscii	3-7	3-7	Spines most prominent on 5th process.	B	Shenoy and Sankolli, 1967
Petrolisthes rufescens	?	?	Not mentioned.	B	Gohar and Al-Kholy, 1957
"Porcellanella" sp.	?	?	Not mentioned.	B	Menon, 1937
Petrolisthes elongatus	3-7	3-7	6 prominent spines, inner margin; less prominent spines, outer margin.	B	Wear, 1964b Greenwood, 1965
Petrocheles spinosus	4,5	4,5	6-8 spines, inner margin.	C	Wear, 1966
Petrolisthes novaezelandiae	3	3,4	5-6 spines, inner margin.	A	Wear, 1964a Greenwood, 1965
?*Petrolisthes* sp. I	?	?	Not mentioned.	A	Menon, 1937
?*Petrolisthes* sp. II	?	?	Not mentioned.	A	Menon, 1937
Porcellana platycheles	3	3	Long fine spines inner margin only (?)	A	Lebour, 1943
Porcellana ornata	3-7	?	"Hooks" minute, most prominent on 3rd process.	A	Sankolli, 1967
Porcellana sigsbeiana	3-7	3-7	Finely dentate	A	Gore, 1971b
Porcellana sayana (as *P. ocellata*)	3-7	?	According to figures, tips are similar, smooth, or finely serrated(?)		Brooks and Wilson, 1883
Pisidia longicornis	3	3	Well-defined spines, equal number inner and outer margins (first 3 species listed).	A	Lebour, 1943 Sars, 1889
Pisidia bluteli	3	3		A	Bourdillon-Casanova, 1956
Pisidia inaequalis	3	3		A	Gurney, 1938
Pisidia spinulifrons	3	?	Minute "hooks", more developed on outer than on inner margin.	A	Sankolli, 1967
Polyonyx gibbesi	0	0		A	Gore, 1968
Polyonyx quadriungulatus	3	3	More spines on outer than on inner margin.	A	Knight, 1966
Polyonyx hendersoni	3-7	?	Minute spines, most prominent on 3rd process.	A	Sankolli, 1967
Euceramus praelongus	3,4	3,4	Well-defined spines, equal number inner and outer margins.	A	Roberts, 1968

[1] A = Lebour's (1943) definition of *Porcellana* telson. Telson about 1½ times as wide as long with seventh pair of processes situated outside and below central prominence in stage I. In stage II, an eighth pair of processes is added on the central prominence.
B = Lebour's (1943) definition of *Petrolisthes* telson. Telson about as long as wide with seventh pair of processes situated on central prominence in stage I. In stage II, a single median spine (or setae) added.
C = Fits neither A nor B exactly.

onyx, *Porcellana*, and *Pisidia*. A third telson type (C, Table 3) has since been described and to date includes only the larvae of *Petrocheles spinosus* from New Zealand.

Among larvae possessing a similar telson form, further systematic separation following generic lines appears to be possible on the basis of the position of the long telson setae (processes 3 through 7) armed distally with conspicuous spines. This is particularly true of 13 larvae of known adult origin possessing the *Petrolisthes* type telson. Of these 13 species, only the larvae attributed to *Pachycheles natalensis* differ from other larvae of the same genus.

The known larvae possessing the *Porcellana* type telson are more difficult to group using telson seta armature alone. Only larvae of the single known species of *Euceramus* can be distinguished from other known larvae of this telson type on the basis of setal armature. In

TABLE 4.—Comparison of larvae of four *Pachycheles* species. (All unlabeled figures are setal numbers; all serial listings are proximal to distal.)

TABLE 4.—Comparison of larvae of four *Pachycheles* species.
(All unlabeled figures are setal numbers; all serial listings are proximal to distal.)

Appendage	Zoea I				Zoea II			
	P. rudis Knight 1966 and this study	*P. pubescens* This study	*P. haigae* Boschi et al., 1967	*P. stevensii* Kurata 1964	*P. rudis*	*P. pubescens*	*P. haigae*	*P. stevensii*
Antennule	3-4 aesthetascs; 1-2 setae	3-4 aesthetascs; 1-2 setae	3 aesthetascs; 2-3 setae	?	biramous; aesthetasc tiers 4, 5, 3, 3, 2	biramous; aesthetase tiers 4-6, 4-5, 3, 3, 2	biramous; aesthetascs 8-14, 3 terminals	
Antenna:								
Endopodite	1 fine seta	0	1 fine seta	1 fine seta	1 seta	1 seta, 2 small spines	1 seta	
Exopodite	3 spines	1-4 spines	4 spines	3 spines	(3) spines rudimentary or absent	0 spines	0 spines	
Mandible	no palp bud	no palp bud	no palp bud	no palp bud	pulp bed present	palp bud present	palp bud present	palp bud present
Maxilla I:								
Coxal endite	9	7-9	8	8	10-11	8-11	10	NOT
Basal endite	9	8-9	9	6	10	9-10	11	
Endopodite	4	3-5	4	4	4	3-4	4	
Maxilla II:								
Coxal endite, PL[1]	6-8	6-9	9	7	9-12	10-13	7-8	MENTIONED
Coxal endite, DL[1]	4	3-5	7	3	6-7	4-7	5-7	
Basal endite, PL	7	6-8	7	5	10-11	9-11	6-7	
Basal endite, DL	7-8	6-8	7	6	10-12	9-11	8-10	
Endopodite	9	8-9	7	9	9	9	5	OR
Scapognathite	6 + 1 apical	7 + 1 apical	8 + 1 apical	6 + 1 apical	20-22	21	21-24	
Maxilliped I:								
Coxopodite	2	2	none?	NOT	2	2	2	FIGURED
Basipodite	2, 2, 2, 3	2, 2, 2, 3	2, 2, 3, 3		2, 2, 2-3, 3	2, 2, 2, 3	2, 2, 2, 3	?, 2, 2, 3
Exopodite	4	4	4		14	14	14	14
Endopodite:								
Inner margin	3, 2, 5, 7-8	2-3, 3, 3-6, 7-9	2, 4, 7, 10	MENTIONED	3, 2, 5, 7-9	3, 3-4, 3-6, 8-11	2, 4, 7, 10	3, 3, 2, 10
Outer margin	0, 0, 0, 1	0, 0, 0, 1	0, 0, 0, 1		0, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1
Maxilliped II:								
Coxopodite	0	0	0		0	0	0	0
Basipodite	1, 2	1, 2	2	OR	1, 2	1, 2	1, 2	1, 2
Exopodite	4	4	4		14	14	14	14
Endopodite								
Inner margin	2, 2, 3, 5	2-3, 2, 3, 5-6	3, 3, 2, 7		2, 2, 3, 5	2-3, 1-2, 2-3, 5	3, 3, 2, 7	2, 2, 1, 5
Outer margin	0, 0, 0, 1	0, 0, 0, 1	0, 0, 0, 1	FIGURED	0, 1, 1, 1	1, 1, 1, 1	0, 1, 1, 1	1, 1, 1, 1
Maxilliped III	bilobed bud	bilobed bud			bilobed; 2 setae	bilobed; 4-6 setae	bilobed; 2 setae	bilobed; 2 setae
Pereiopods	5 pairs buds	5 pairs buds			5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate
Abdomen	5 segments, no pleopods	5 segments, no pleopods	5 segments, no pleopods	5 segments, no pleopods	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5
Primary chromatophores	Total 3	Total 7	Total 5?	?	Total 3	Total 7	Total 5(?)	?

[1] PL = proximal lobe.
DL = distal lobe.

TABLE 5.—Comparison of maxilliped setation in *Petrolisthes cinctipes* and *P. eriomerus*. (All serial listings are numbers of setae, arranged proximally to distally.)

Appendage	Zoea I		Zoea II	
	P. cinctipes	*P. eriomerus*	*P. cinctipes*	*P. eriomerus*
Maxilliped I:				
Coxopodite	1-2	2	1-2	2
Basipodite	2, 2, 3, 3	2, 2, 3, 3	2, 2, 3, 3	2, 2, 3, 3
Exopodite	4	4	14	14
Endopodite:				
Inner margin	1-3, 2-3, 4-7, 5-7	2-3, 3, 5-6, 5-7	3, 3, 5, 5-6	2-3, 3-4, 5, 4-7
Outer margin	0, 0, 0-1, 1	0, 0, 0, 1	0, 1, 1, 1	0, 1, 1, 1
Maxilliped II:				
Coxopodite	0	0	0	0
Basipodite	1, 2	1, 1-2	1, 2	1, 2
Exopodite	4	4	14	14
Endopodite:				
Inner margin	1-2, 1-2, 2-3, 3-5	1-2, 1-3, 3-4, 3-5	2, 2, 3, 4-6	1-2, 2, 3-4, 5
Outer margin	0, 0, 0, 1	0, 0, 0, 1	1, 1, 1, 1	0, 1, 1, 1

contrast, larvae belonging to species of the present genera *Porcellana*, *Pisidia*, and *Polyonx* exhibit several different patterns of armed telson setae, a fact which, when coupled with the confusion of adults of these genera in the past, suggests that systematic problems still exist among these groups. The only point worth noting at this time is that second zoeae of two of the three species currently bearing the genus name of *Pisidia* and the second zoea of *Petrolisthes novaezelandiae*, which Wear suggests is actually a *Pisidia*, all have similar setal armatures and possess three pairs of pleopod buds on the abdomen. All other porcellanid zoea II larvae known to species have four pairs of pleopod buds. In order to determine whether these two characters are of any value in distinguishing the larvae of the genus *Pisidia* from other larvae with the *Porcellana* type telson, the second zoea of *Pisidia spinulifrons* must be described, the identity of Menon's (1937) "*Petrolisthes*" species I and II, with three pleopod pairs, resolved and *Pisidia inaequalis*, with four pleopod pairs, reexamined as a member of the genus.

In the course of this study, a number of specimens of each stage were examined, and particular attention paid to morphological variation, especially in setal counts for the larval appendages, since larval variability has caused a great deal of confusion in the literature on porcellanid and other anomuran larvae. Morphological variations in setal numbers, spine lengths, etc. were found within individuals from the left to the right sides, between individuals of the same species, and between individuals of the different species studied. These findings emphasize the necessity of basing larval descriptions, especially setal counts, on examination of adequate numbers of larvae of each stage. Throughout the descriptions given here, only the range of setal numbers found is indicated. Because of the importance placed on setation formulae in descriptions of crustacean larvae, some of the setal count variations found and their implications will be analyzed in a separate paper.

Variability in the number of larval molts required to reach a specific point in development, apparently in response to varying environmental conditions, occurs in many Anomura (Table 6) and other decapod groups as well (e.g., Broad, 1957; Costlow, 1965). This type of variation has caused difficulties among larval systematists for some time and has in part given rise to the idea that either larvae produced under laboratory conditions are abnormal and should be discounted altogether or that such stages are extraneous and should be subgrouped under larval stages most commonly noted. This concept of substages or extra stages has served to confuse the developmental picture (Efford, 1970), particularly among the porcellanids, where another type of variability has been discovered which, unfortunately, has lent further support to the "substage" concept.

Intermolt growth in which certain appendages increase in size within a single larval stage without molt is a type of variability prevalent in porcellanids. All four species described here show

this type of growth. Lebour (1943, 1950) was probably the first author to notice specimens showing this phenomenon. Lebour observed some substage molting and concluded that each substage she found in plankton collections must necessarily have been separated from less advanced substages by a discrete molt. She subsequently proposed that *Pisidia longicornis* and *Porcellana platycheles* probably possessed a variable number of stages with two "essential" stages. She assumed that a molt always separated the "alternative" stages, or substages from each other. The variable molting sequence may indeed occur in these species under certain circumstances, as it does in other Anomura (Table 6), but it is probable that Ib and IIc substages in *Pisidia longicornis* and IIc in *Porcellana platycheles*, which were taken in plankton samples but never obtained by molt in the laboratory, were products of intermolt growth.

LeRoux (1961, 1966) subsequently reared the larvae of both species and reported only two "true" zoeal stages each of which underwent growth in certain appendage buds without molting. It is likely that these species have the potential for both intermolt growth and stage number variability and that Lebour found a combination of both while LeRoux did not. A similar case might also exist in the *Petrolisthes* larvae studied by Wear (1964a, b), although he reports definite ecdysis between each of his substages. Larvae of these species, like the *Pisidia* and *Porcellana* species mentioned above, may show both intermolt growth and variable stage numbers, depending on environmental circumstances, a possibility not considered for example, by Roberts (1968) and Gore (1970) in discussing substages.

Other authors have subsequently supported Lebour's original substage designation of growth forms even though no molting was observed (e.g., Boschi et al., 1967). This is a needless and confusing subdivision of an apparently continuous process and it obscures the nature of the flexibility of the animals. The term substage is now used in such a variety of ways that it should be abandoned altogether, as Gore (1970) has suggested, and attention directed to the possible occurrence of variation in both molting and development rates as observed by Costlow (1965) in the portunid *Callinectes sapidus*.

Intermolt growth to date has been recorded directly or indirectly in the larvae of 70% of the porcellanids studied for which two or more zoeal stages are known (Table 7). All these species have demonstrated abbreviated development (fewer number of molts necessary to attain juvenile adult form) compared to most other

TABLE 6.—Species of Anomura other than Porcellanidae for which stage number variability has been reported.[1]

Species of Anomura	Source
Pleuroncodes planipes	Boyd and Johnson, 1963
Emerita talpoida	Rees, 1959
Emerita analoga	Johnson and Lewis, 1942; Efford, 1970
Emerita rathbunae	Knight, 1967
Hippa cubensis	Hanson, 1969
Blepharipoda occidentalis	Knight, 1968; Johnson and Lewis, 1942
Calcinus tibicen	Provenzano, 1962a
Coenbita clypeatus	Provenzano, 1962b
Trizopagurus magnificus	Provenzano, 1967
Petrochirus diogenes	Provenzano, 1968
Birgus latro	Reese and Kinzie, 1968
Paralithodes camtschatica	Kurata, 1960

[1] Intermolt growth has not been reported in the larvae of any of the above species.

TABLE 7.—Species of Porcellanidae for which intermolt growth or stage number variability have been reported. Includes only species with both zoeae known.

Species	Intermolt growth[1]	Stage variability[1]	Author
Petrolisthes cinctipes	+	–	This study
Petrolisthes eriomerus	+	–	This study
Petrolisthes armatus	–	+	Gurney, 1938
	–	+	Lebour, 1943, 1950
	+	–	Gore, 1970, 1972
Petrolisthes elongatus	O	+	Wear, 1964b
Petrolisthes novaezelandiae	O	+	Wear, 1964a
Petrolisthes rufescens	O	–	Gohar and Al-Kholy, 1957
Petrolisthes sp. I	O	–	Menon, 1937
Petrolisthes sp. II	O	–	Menon, 1937
Porcellana sp.	O	–	Menon, 1937
Porcellana platycheles	+	–	Le Roux, 1961
	–	+	Lebour, 1943
Porcellana sigsbeiana	+	–	Gore, 1971b
Pisidia longicornis	+	–	Le Roux, 1966
	–	+	Lebour, 1943
Pisidia bluteli	O	–	Bourdillon-Casanova, 1956
Pisidia inaequalis	O	–	Gurney, 1938
Polyonyx gibbesi	+	–	Gore, 1968
Polyonyx quadriungulatus	+	–	Knight, 1966
Pachycheles pubescens	+	–	This study
Pachycheles rudis	+	–	Knight, 1966; this study
Pachycheles haigae	+	–	Boschi et al., 1967
Pachycheles stevensii	+	–	Kurata, 1964
Euceramus praelongus	+	–	Roberts, 1968
Petrocheles spinosus	–	–	Wear, 1965a
Megalobrachium poeyi	+	–	Gore, 1971a

[1] + = Occurrence reported.
– = Occurrence not reported.
O = Occurrence probable but not directly reported.

Anomura studied but not necessarily reduced time spent in the plankton. This suggests that intermolt growth might permit larvae of these species to develop to metamorphosis under a variety of conditions without passing through a large number of molts. This mechanism might thus be of survival value in reducing larval loss at molt by effectively decreasing the number of molts required under various conditions to reach the juvenile form.

As more larval histories are studied, it may be found that intermolt growth occurs in Anomura other than the Porcellanidae. If the function and value of intermolt growth has been correctly interpreted here, this form of variability might be expected among species with low numbers of larval molts required to attain the subadult. Only careful studies of more life histories can reveal the possible relationship of intermolt growth and variable stage numbers.

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FEEDING, CLEANING, AND SWIMMING BEHAVIOR IN LARVAL STAGES OF PORCELLANID CRABS (CRUSTACEA: ANOMURA)[1]

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ABSTRACT

Pachycheles rudis, *Pachycheles pubescens*, *Petrolisthes eriomerus*, and *Petrolisthes cinctipes* have a swimming prezoeal stage of short duration. The prezoeal form is probably related to escapement of the larvae from the confined adult habitat.

Both zoeal stages are strong swimmers, moving both forward and backward by means of the maxillipedal exopodites, aided by the telson. Zoeae have a well-defined cleaning behavioral sequence for removal with the mouth parts of particles from the telson and the maxillipedal endopodites. The two zoeal stages are carnivorous and capture live prey upon contact but do not appear to locate prey visually. Prey are caught with the maxillipedal endopodites and held with the flexed abdomen and telson.

At the molt to megalopa, the larva becomes a filter-feeding herbivore like the adult. Other adultlike behavior of the megalopa includes use of the fifth legs for cleaning and attempts by older megalopae at swimming by clapping the abdomen. Megalopae filter feed only when suspended algal food is present; water movement enhances feeding but is insufficient alone to induce feeding. At first, using their abdominal pleopods, megalopae swim continuously, later swim intermittently, and finally settle permanently if a substrate suitable for clinging is available.

A large amount of information is available about the comparative larval morphology of most groups of decapod Crustacea. Further understanding of the adaptive significance of larval morphology and its changes during larval life requires comparable information, now largely lacking, about larval behavior and ecology. The present state of knowledge on the larvae of porcellanid crabs is typical in this respect, with a growing descriptive literature available but little known about other aspects of larval biology. A few observations on various features of porcellanid larval behavior have been given by Russell (1925), Spooner (1933), Foxon (1934), Gurney (1942), Lebour (1943), Greenwood (1965), and Knight (1966). None of these studies present a complete account of any behavior pattern throughout development. Information on food and feeding is incomplete and somewhat inconsistent. The detailed studies on feeding and respiration of adults by Nicol (1932) and Knudsen (1964) indicate that adult porcellanids are specialized filter feeders. The available information indicates that zoeae are carnivorous or possibly also detrital feeders. Since it is now known that decapod zoeae are typically strict carnivores capturing live prey, a change in diet and mode of feeding during the development of porcellanids would be expected, but has not been clearly described.

Large numbers of live larvae of all developmental stages and ages were available in laboratory cultures during a study of the larval development of four species of porcellanid crabs (Gonor and Gonor, 1973). Several aspects of the behavior of the larvae being cultured were studied closely throughout development. Special attention was given to the ontogeny of normal respiratory, feeding, cleaning, and locomotory behavior patterns from hatching through development to the first juvenile crab stage. These

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observations are presented here to clarify some aspects of the ecology of both the larval and adult stages.

METHODS

The species used were *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles rudis* Stimpson, and *Pachycheles pubescens* Holmes. Adults of all of these species occur in the rocky intertidal or the shallow subtidal zone of the northeastern Pacific but their habitats differ (Haig, 1960). The *Petrolisthes* species occur in the upper intertidal beneath loosely bedded rocks and boulders, whereas the two *Pachycheles* species are crevice and burrow dwellers. *P. rudis* was collected from beneath root mats of the surf grass *Phyllospadix* in the lower intertidal zone and *P. pubescens* was collected from burrows and crevices in rocks. Both larvae captured alive in the plankton and larvae reared from eggs carried by females in the laboratory were available.

Gravid females were maintained in the laboratory at ambient sea temperatures until hatching occurred. Thereafter, larvae were cultured in filtered seawater kept at several constant temperatures and fed *Artemia* nauplii. Larvae captured in the plankton were similarly maintained in the laboratory. A detailed account of methods used in rearing and handling the larvae is given elsewhere (Gonor and Gonor, 1973).

RESULTS

In laboratory cultures, larvae of each of the four species showed similar basic patterns of locomotion, feeding, respiration, and cleaning, as well as changes in these patterns through time. Consequently, separate accounts for each species will not be given. Basic body and appendage form is sufficiently similar in the first and second zoeae for Figures 2 and 3, of second zoeal appendages, to be referred to in the text for both stages. The descriptions given below are summarized from observations repeated throughout the rearing study as each of the cultures was examined daily. Table 1 gives the number of larvae of each stage kept in culture for at least 2 days, and available for observations on behavior at some time during the 2-year period of the study.

PREZOEA

Females of all four species studied here release their larvae in the form of a prezoea (Figure 1).

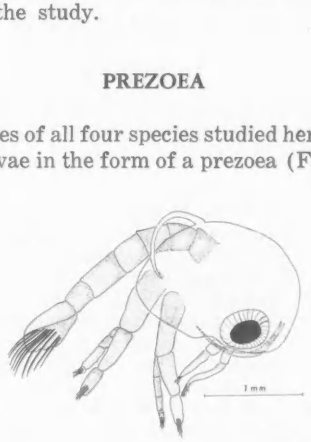

FIGURE 1.—Prezoea of *Pachycheles pubescens*, showing rounded form.

Gravid females were maintained in the laboratory for as long as 35 days, showing normal locomotion, feeding, and cleaning behavior before their eggs hatched. The following numbers of broods were hatched in the laboratory: *Pachycheles rudis*, 35; *P. pubescens*, 2; *Petrolisthes eriomerus*, 11; *P. cinctipes*, 10. In each case female behavior during hatching was of the normal type described elsewhere (Gonor and Gonor, 1973), and the larvae released were prezoeae which molted to viable first zoeae. The behavior patterns of the prezoea are simpler than those of later stages. Respiratory motions in the prezoea are effected by the fanlike scaphognathite of the second maxilla. The type of

TABLE 1.—Number and source of larvae of different stages available for behavioral observations.

Species	Zoea I	Zoea II	Megalopa
Petrolisthes cinctipes (reared)	727	19	1
Petrolisthes eriomerus (reared)	603	58	14
Pachycheles rudis (reared)	757	21	1
Pachycheles rudis (plankton)	76	58	28
Pachycheles pubescens (reared)	100	18	--
Pachycheles pubescens (plankton)	26	81	36
Total	2,289	255	80

cleaning behavior described below for the zoeal stages has not been observed in this stage. It probably is not present since the stage is short-lived and the major natatory and telson setae are confined beneath the larval cuticle.

Prezoeal locomotion consists of violent spasmodic flexions of the abdomen, and there is no feeding during this stage. The larva appears to be only slightly photopositive. The strong abdominal flexions finally split the cuticle longitudinally along the dorsal midline of the carapace just behind the point where the rostrum joins the carapace, and a first zoea emerges from the thin prezoeal cuticle.

ZOEAL STAGES

The behavior patterns of the first true zoea are considerably more complex than those of the prezoeal stage. Respiratory currents are still produced by the beating of the maxillae and are aided by swimming, as was also noted by Foxon (1934). Detrital particles often become entangled in the plumose setae of the maxillipeds and telson. Cleaning behavior is simple but well defined in this stage. The telson and the plumose setae along its posterior margin are cleaned by curving the abdomen under the thorax and dragging the telson posteriorly across the functional mouth parts, thus loosening and scraping off clinging debris. This scraping also serves to remove large pieces of detritus from the peripheral setae on the mouth parts and from the setae of the endopodites on both sets of maxillipeds. The endopodites are used in feeding and require frequent cleaning. Direct cleaning of the exopodites and natatory setae and of the carapace spines was never observed, however. The cleaning observed was indirect and probably accidental, since it consisted simply of freeing the body surface of entangled debris by larval motion and reversal of swimming direction.

The first zoea swims primarily by beating the maxillipedal exopodites (Figure 2) which have long natatory setae, but this may be augmented by motions of the telson. The maxilliped endopodites are held extended ventrally and do not function in swimming. The zoea are strong swimmers and due to the configuration of the

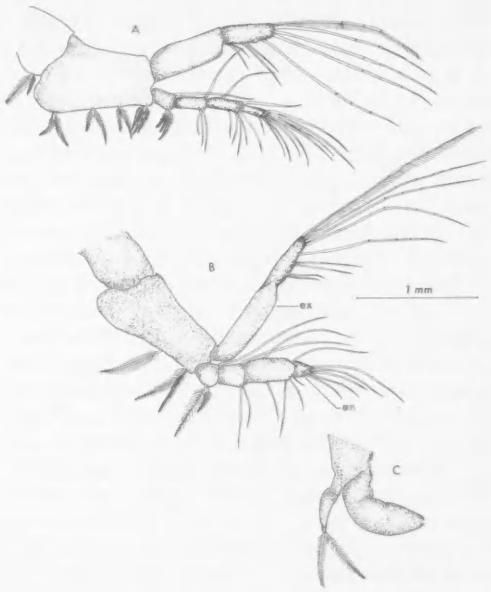

FIGURE 2.—Maxillipeds of Zoea II, *Pachycheles pubescens*, with setules omitted from most plumose setae. Ex - exopodite; en - endopodite; A - Maxilliped I; B - Maxilliped II; C - Maxilliped III.

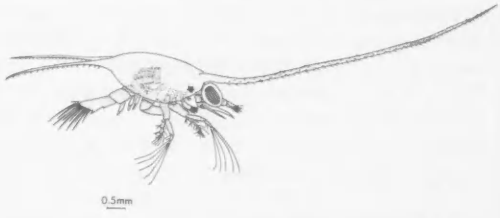

FIGURE 3.—Zoea II of *Pachycheles pubescens*, in forward swimming posture. Maxillipeds I and II rotated slightly for clarity.

carapace spines (Figure 3), swim predominantly backward and forward.

Forward motion is accomplished by synchronously beating both sets of exopodites downward and posteriorly, with the telson extended posteriorly. Reversal of direction can be achieved very quickly by a forward snap of the telson and a

simultaneous change in the pitch of the maxillipeds so that the exopodites beat downward and anteriorly. This rapid adjustment sends the larva on its way backward with its posterior spines leading. Unlike some larvae of the Galatheidae (Foxon, 1934), which swim only backward with the telson leading, the zoeae of porcelain crabs swim almost equally well in either direction. Normally, zoeae swim forward, reversing direction on contact with an object.

Zoea larva are voracious predators and are cannibalistic if not well supplied with other types of food. However, true hunting behavior of the kind reported for certain other predatory zoeae (Knudsen, 1960) was not observed. In fact, when a potential food organism touches any portion of the rostrum or posterior spines, or the top or sides of the carapace, the zoea immediately moves away from the point of contact, apparently in an act of avoidance. If, however, the prey approaches the thoracic region of a zoea closely enough to touch the setae of the ventrally extended maxillipedal endopodites (Figures 2, 3) or the ventral surface of the first two segments of the abdomen, the zoea reacts immediately. The prey is clutched between the endopodites, and the telson is used to force it forward and upward within reach of the functional mouth parts. This sequence has been observed many times, with no indication that sight is involved in locating and capturing the prey. The zoea also demonstrates what appears to be sensitivity to water movements. If a prey organism passes near the thoracic or abdominal region of the zoea but does not touch the sensitive setae, the zoea, without the stimulus of direct contact, will go through all the motions normally associated with the capture of prey. In these cases, the prey is usually out of reach, and the attempts to capture the passing animal fail.

The second zoeal stage is only slightly more complex morphologically than the first stage, and behavior patterns remain essentially the same throughout both zoeal stages. Metamorphosis to the megalopa (Figure 4), however, brings about immediate and drastic changes in structures and habits of the larva. Basic behavior patterns which were stable in the zoeal stages undergo progressive changes throughout the megalopa stage, gradually becoming more adultlike in nature.

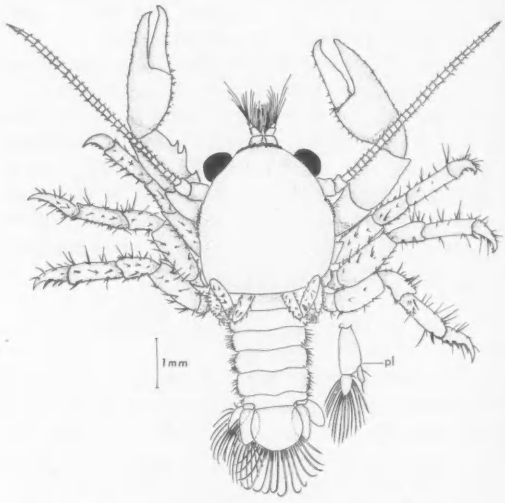

FIGURE 4.—Megalopa of *Pachycheles pubescens*, in forward pleopodal swimming posture, except antennae not extended posteriad. Pl, detail view of pleopod.

MEGALOPA

In the megalopa respiratory currents are produced primarily by fanning motions of the maxillary scaphognathites (Figure 5C) and are aided by the outward flicking of the setose exopodite of maxilliped II (Figure 5B). The outward flicking causes an exhalent current by "spooning out" the branchial cavity. The exopodite of maxilliped III is nonfunctional at this stage. In addition, a newly settled larva elevates its body above the substrate and concurrently vibrates its pleopods (Figure 4), thus increasing circulation of the surrounding water.

Cleaning behavior becomes highly complex in the megalopa. The fifth pereiopods (Figure 4), which are mobile, chelate, and armed with specialized hooked setae and dense clusters of short bristles, are carried folded along the sides of the carapace when not in use. These structures serve to clean all portions of the abdomen and telson, the three pairs of functional walking legs,

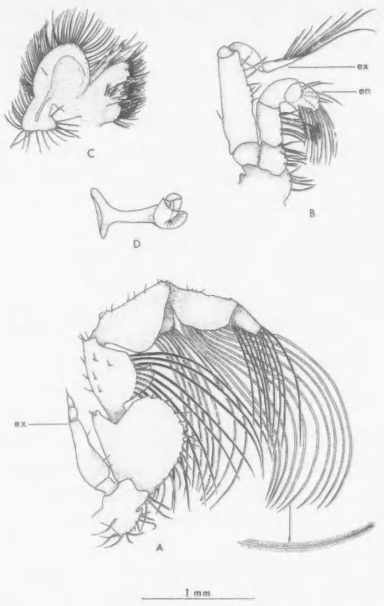

FIGURE 5.—Megalopa respiratory and feeding structures *Pachycheles pubescens*. Setules omitted from all plumose setae. Ex - Exopodite; en - endopodite; arrow - detail of a plumose seta. A - Maxilliped III; B - Maxilliped II; C - Maxilla II; D - mandible, anterior view, palp folded in place.

and the under side of the carapace in the branchial chamber. The foremost one-fourth of the carapace cannot be reached by these legs, and in dense algal suspensions, fine hairs on this portion of the megalopa may become entangled with algae and other detritus.

The chelipeds are freed of foreign matter by rubbing the dorsal surface of one on the ventral surface of the other in a simple lateral scraping motion. The antennules are cleaned singly or simultaneously in the following manner. An antennule is lowered to the level of a raised third maxilliped and inserted into a notch on the maxilliped formed by a long and a short group of dense setae. The setae and aesthetes of the antennule are then effectively combed free of particles as the maxilliped is drawn forward and down and the antennule passes between the setal brushes.

The grooming of the feeding mechanism is the most complex cleaning behavior. This behavior can be seen in actively feeding animals as well as in nonfeeding megalopae which have been placed in a dense suspension of algal cells. The long feeding setae of the third maxilliped (Figure 5A) are combed clean by the short dense setal brushes located on the two terminal segments of the second maxilliped (Figure 5B). The short setal brush is inserted at the bases of the feeding setae and rolled downward and inward toward the mouth following the long curve of the setae being combed. When the entire length of the filtering setae has been combed free of particles, the brushes of the second maxilliped are then combed out by the first maxilliped and inner mouth parts. Undesirable particles are rejected into the exhalent current and swept out by the flicking of the exopodite on maxilliped II.

The diet and feeding behavior of the megalopa are drastically different from those of the zoeal stages. Predatory habits are replaced immediately by filter-feeding habits when the molt is completed and the megalopal skeleton has become hard enough to permit motion. The megalopae of all four species rejected newly hatched *Artemia* nauplii as food and would feed only on suspended phytoplankton. Several monoalgal and diatom cultures (*Tetraselmis* sp., *Isochrysis* sp., and several unidentified diatoms) and nutrient culture medium inoculated with raw seawater were tried singly and in various combinations as food. In each case the megalopae fed on the suspended organisms in the cultures in the same manner.

The behavioral change from prey capture to suspension feeding is reflected in changes in mandibular and maxilliped form. The natatory second maxilliped and the functionless third maxilliped of the zoea become highly specialized parts of a complex feeding mechanism in the megalopa. The feeding pattern most commonly observed in the laboratory is composed of the following sequence of events.

The endopodite of the highly setose third maxilliped is extended and a "setal net" spread open. After a moment, the maxilliped is lowered and swung in toward the body, where the setae are

combed out by the process described earlier. The terminal brushes of the second maxilliped are subsequently cleaned by the first maxilliped and so on, until the particles initially trapped in the extended net finally reach the mandibles. Somewhere in this chain of events particles are sorted, and undesirable portions of the catch are ejected in the exhalent respiratory stream. Particles which are acceptable as food are ground up between the curved bladelike edges of the mandibles (Figure 5D) and passed into the mouth with the aid of the mandibular palp.

Most often the maxillipeds work rapidly and alternately, with one extended while the other is being combed. However, when a strong current of water runs steadily from a single direction, megalopae often extend only one maxilliped and leave it out for a time. When the setae have gathered a sufficient quantity of particles, the maxilliped is withdrawn and cleaned. At this point, the free maxilliped may be extended, or the same maxilliped may be extended again after it has been cleaned. The appearance of variable feeding behavior under varying conditions led to the question of the importance of water movement to megalopal feeding.

A 36-hr experiment was conducted in an effort to determine the effect of turbulence on feeding. Eighteen healthy megalopae, nine each of *Pachycheles rudis* and *P. pubescens*, were used. Each of the megalopae and a stone for it to cling to were placed in a flask of filtered seawater and starved for the first 13 hr of the experiment. A mixed algal suspension of *Isocrysis* sp. and *Tetraselmis* sp., previously found to be acceptable to megalopae as food, was supplied to the same 18 larvae for the remaining 24 hr of the experiment. At intervals of 2 hr, throughout the 36-hr period, the number of animals showing feeding motions was recorded before and after stirring the water. The flasks with the megalopae were held at 12°C in a water bath. The experiment was started at 0100 on one day and continued to 1300 the next before food was introduced, so that observations were made for both starved and fed conditions at night and during daylight hours.

Figure 6 summarizes the observations on the number of animals feeding under each condition, before and after stirring the water. When no food was present and the water was still, virtually no feeding activity was observed.

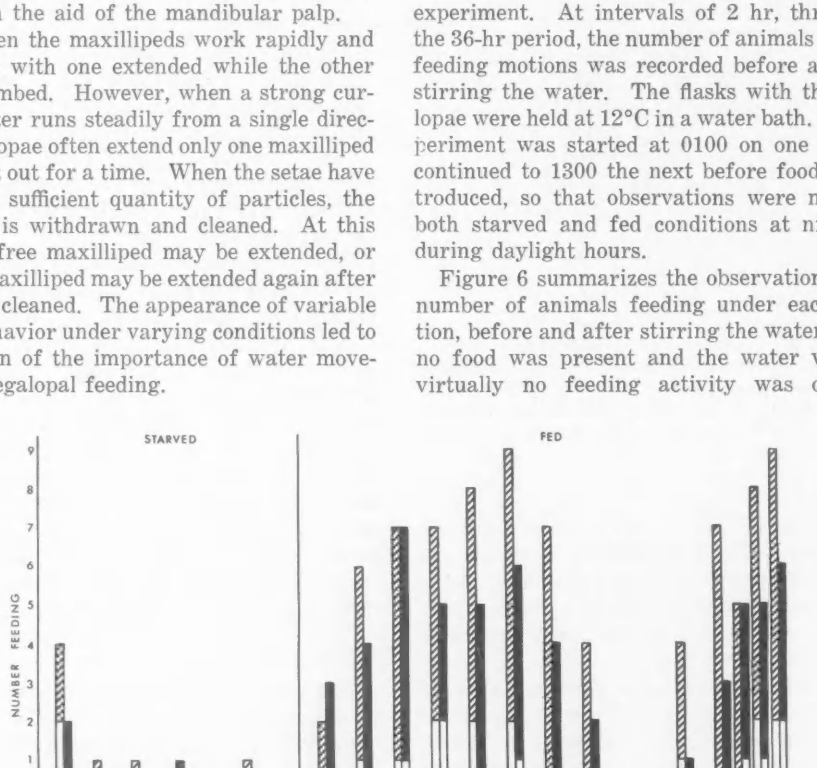

FIGURE 6.—Histogram showing effect of water movement on feeding behavior in megalopae of *Pachycheles pubescens* and *P. rudis* under starved and fed conditions. Left bars, *P. pubescens;* lower, open part of bar, number of larvae feeding in still water; cross-hatched part of bar, number feeding after agitation of water. Right bars, *P. rudis*; open part of bar, number of larvae feeding in still water; solid part of bar, number feeding after agitation of water.

Turbulence caused a few animals to undergo feeding behavior even when food was absent. When food was present, there usually was some feeding activity in still water. When the water was agitated and food was present, feeding behavior greatly increased. In the presence of food, water movement, although not essential for the initiation of feeding, favors both the initiation and maintenance of feeding activity, probably because turbulence suspends the particles so that they can readily be filtered. The results suggest that there is a periodicity to feeding activity, but the experiment was too brief to clearly demonstrate this. No effect of daylight or darkness on feeding behavior was observed.

Locomotory behavior gradually changed throughout the megalopa stage. The numbers of megalopae available for observation at different ages are indicated in Table 2, which gives the age of the megalopae in days since the molt from the second zoeal stage. Adultlike locomotory behavior slowly evolved as the megalopa grew older. Newly metamorphosed megalopae were strongly planktonic, swimming almost continuously by means of the pleopods, with the walking legs and chelipeds extended forward. After spending some time (1-4 days) as truly planktonic animals, the megalopae became more quiescent and began to demonstrate clinging tendencies. Small stones, to which the settling megalopae could cling, were introduced into the culture flasks at this point.

The megalopae which are just beginning to settle show no signs of recognizing a substrate suitable for settling. If a larva encounters a rock while swimming forward, it continues swimming motions, pushing against the obstacle with the extended chelipeds but not moving forward. However, if megalopae of this age are artificially introduced to a rough surface, walking legs first, by means of turbulence or by direct placement, they cling readily and will usually remain on that surface unless disturbed. As the megalopae increase in age, they appear to develop the ability to recognize a suitable substratum. Larvae of 2 weeks or older were seen to collide head on with a rock, stop swimming, and put the walking legs down. They then turned around and backed onto the piece of gravel.

In the laboratory, recently settled megalopae can be induced to leave an apparently suitable substrate if the water is stirred vigorously or if the larvae are touched. In addition, when a settling megalopa encounters a stone that is already occupied, it will remain there only if it can do so without contacting the other occupant. If the stone is too small to allow this, the settling megalopa will usually cling only momentarily and then resume swimming. In a few cases, however, the settling megalopa forced the original occupant to leave its stone and begin swimming.

A specialized form of behavior was observed in advanced megalopae of *Petrolisthes eriomerus*. After locating a stone, a swimming megalopa will settle on it and then elevate and lower both chelipeds simultaneously several times. If the megalopa then moves a short distance over the rock, the cheliped elevation sequence is often repeated. This activity was observed only in individuals that had just arrived on a substrate and was exhibited whether or not another megalopa was present on the rock.

An advanced behavior was observed in still older animals (30-33 days in *Pachycheles pubescens*). These megalopae could not be induced to use their pleopods when swimming, even when they were so disturbed that they would finally leave their rocks. Instead, a disturbed animal would bob up and down in the water, clumsily clapping the abdomen to the thorax. The presence of the four pairs of fully developed pleopods prevented effective swimming by this action. Adult porcelain crabs, whose pleopods are reduced in size and often in number, swim only by clapping the abdomen to the thorax. The

TABLE 2.—Number and age in days of megalopae available for behavioral observations.

Species	Age in days							
	5	10	15	20	30	40	45	50
Pachycheles pubescens	34	32	27	25	18	9	4	
Pachycheles rudis	21	19	17	17	11	4	3	1
Petrolisthes eriomerus	14	8	7	1				
Petrolisthes cinctipes	1							
Total	70	59	51	41	29	13	7	1

megalopae therefore show in this situation the behavior of adults.

Further development along the lines already established by the megalopa is shown by the succeeding juvenile stages. Respiratory currents become much stronger and well defined and are now aided by the tandem motion of the two sets of maxillipedal exopodites. Feeding movements are the same as those described here for the megalopa and for the adult by Nicol (1932). In adults, food preferences vary according to species. Knudsen (1964) reports that pelagic diatoms are the preferred food for *Petrolisthes eriomerus* but does not state the preferences of *Pachycheles rudis*. In the laboratory, adults of all species readily fed in unfiltered seawater, but only *Petrolisthes* females accept and ingest fragments of mantle and adductor muscle of *Mytilus*. The preferred adult locomotion is pereipodal walking, but swimming by abdominal clapping is also used, especially in *Petrolisthes*.

DISCUSSION

PREZOEA

Adults of both *Petrolisthes* species live where the larvae are released into turbulence caused by waves and currents. These conditions favor the presence of a short-lived, rounded initial larva with few body projections, that would more readily escape entangling algae and debris in the intertidal zone.

The habitats of the two *Pachycheles* species (Haig, 1960) more strongly favor a compact, rounded, initially spineless larval form. In many cases adults become so large that they are unable to pass out through the openings of the burrows or crevices they inhabit. Larvae are released within the adult burrow and must escape this confinement to survive. The prezoeal cuticle covering the telson in *P. pubescens* larvae is well modified for swimming. This was described by Gurney (1942) for other decapods and by Lebour (1943), Wear (1965), and Greenwood (1965) for other porcellanids.

These observations suggest that in the four species considered here, and probably in the family as a whole, the prezoea is a short-lived natural stage and is not a laboratory artifact as has often been suggested. Its existence as a transport stage is ecologically consistent with the natural habitat of the adults. Similar arguments have been put forth by Gore (1968) in defense of the interpretation of the prezoea as a natural stage in the commensal porcellanid *Polyonyx gibbesi*, which releases larvae from inside the tube of the polychaete *Chaetopterus*. Another observation supporting this argument is that, under laboratory conditions, true zoeae, with their long spines, respond very unfavorably to collisions, spine breakage, and collection of detrital material on the spines, all of which would be likely to occur in nature if full zoeae emerged from the eggs and were released into the adult environment. Photopositive swimming behavior would also prove useful to prezoeae released in burrows and crevices, and the larvae studied showed a photopositive response. This response was, however, weak under laboratory conditions.

ZOEA

With the passage of the larva through the prezoeal molt, the first true zoea emerges and becomes an actively swimming planktonic carnivore. Despite the good swimming ability and well-developed eyes of the zoea, no evidence of true hunting behavior was found. Instead, the larvae appear to rely entirely on chance encounters with prey, with capture behavior initiated by direct contact or by vibrations stimulating the maxillipedal endopodites and setae and the ventral surface of the abdomen. Similar stimulation of other parts of the body elicits an escape response by the zoea. Survival of these zoea in the plankton is probably highly dependent upon suitable prey density. The method of prey capture used by these larvae, involving the use of the telson to scoop up the prey and hold it from below, appears to be a feeding method used by zoea throughout the Decapoda. Knudsen (1960), for example, describes this method of feeding in xanthid Brachyura.

MEGALOPA

Many of the adult behavioral features described by Nicol (1932) appear in the megalopa

when the structures used first resemble those of the adult, but before the adult mode of life is adopted. Attempted swimming by abdominal clapping is an example of the development of an adult behavior pattern before the adult structure is completed. Megalopae of these four species clean the body with the fifth legs in the adult manner, a feature also observed for other porcellanid megalopae by Lebour (1943) and Knight (1966).

At the molt to megalopa there is an abrupt change from carnivorous to a filter-feeding, herbivorous habit. As Nicol (1932) first noted, adult Porcellanidae are specialized for filter feeding on suspended material. Adults of the two *Petrolisthes* species studied here will also sometimes accept pieces of mussel as food, but the two *Pachycheles* species will not. The observations on the megalopae of these species and those of Lebour on *Porcellana* species, indicate that the acquisition of morphological and behavioral adaptations to filter feeding in the Porcellanidae involve both the adult and megalopa stages. Although many other anomuran adults feed on particulate material by some mode of filter feeding, it is not known whether this also involves the late larval stages. No information could be found in the literature on feeding by their postzoeal stages. In hermit crabs, which are more generalized detrital-feeding Anomura, both zoea and postzoeal stages can be reared on *Artemia* nauplii, as found for example by Provenzano (1962).

Since population and species success depends upon the megalopae locating a suitable adult habitat, settling behavior is a critical part of later larval development. Settling behavior of barnacles, bryozoa, and some other forms has been studied; however, similar settling behavior in decapod Crustacea has not been studied, with the exception of shell selection by the glaucothoe stage of hermit crabs (Reese, 1962; Hazlett, 1971) and the coconut crab *Birgus latro* (Reese, 1968). For the megalopae studied here, the behavioral sequence of the true planktonic period, the settling and swimming period, and the period of final settlement seems to be highly specialized for substrate selection. Possession of this behavioral mechanism would permit, under natural conditions of turbulent water movement, older megalopae to select or reject substrates encountered by random contact. No information is available on how settled megalopae reach the final adult habitat after initial settlement, but postsettling megalopae and very young juveniles have been found clinging to the base of surf grass and under stones with adults.

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BIOLOGY OF THE PYGMY SEA BASS, *SERRANICULUS PUMILIO* (PISCES: SERRANIDAE)

ROBERT W. HASTINGS[1]

ABSTRACT

During the period from 1968 to 1971, numerous specimens of *Serraniculus pumilio*, were collected in shallow waters of the northern Gulf of Mexico. This paper presents biological data accumulated from these and other specimens in the fish collection of Florida State University and from scattered literature references regarding the species. The range of *S. pumilio* extends from North Carolina along the continental margin of the western Atlantic Ocean to Guyana, but it apparently does not occur in the West Indies. It has been collected at depths from 1 to 117 m, usually over sand or shell bottoms near coral or rock reefs or accumulations of mollusk shells. Individuals move about considerably, although they spend much time resting on the bottom. *S. pumilio* is a synchronous hermaphrodite, but pairs mate to exchange gametes and self-fertilization probably never occurs. Spawning occurs between March and August or September in the northern Gulf of Mexico. A length-frequency distribution of specimens collected in the northern Gulf is presented to show the growth rate of first year fish. Juveniles (15-20 mm SL) which appear inshore in September reach a size of 50-55 mm by the following June. Most fish move offshore to deeper water for the winter (January and February) and individuals larger than 55 mm apparently never appear inshore. Small crustaceans are the most important food items.

Since the pygmy sea bass, *Serraniculus pumilio*, was described in 1952 by Ginsburg, virtually nothing has been added to our knowledge of the species except for a few brief notes in general surveys of fishes. During a study of reef fishes in the northern Gulf of Mexico from 1968 to 1971, numerous specimens of *Serraniculus* were collected and notes were taken on their biology. The present paper is a synopsis of the information scattered in the literature and the new data accumulated during this study.

The generic allocation of the species used in this paper is tentative. Robins and Starck (1961) briefly discussed the characteristics of the genus *Serraniculus* but did not include the species in their review of the genus *Serranus*. Ginsburg (1952) noted that *Serraniculus* and *Dules* differ from *Serranus* in having six rather than seven branchiostegal rays, and that *Dules* differs from the other two genera in having the third dorsal spine greatly prolonged. After subsequent study Robins (personal communication) believes that *Serraniculus* is inseparable from *Dules*, but because *Dules* itself is so close to *Serranus*, he recommends no change until a morphological study of a wider range of serranid genera can be completed. According to Robins, *Serraniculus pumilio* and *Dules auriga* are distinct species.

METHODS

During the present study, 106 specimens of *Serraniculus pumilio* [15.8-54.1 mm standard length (SL)] were collected. Most of these (75) were collected at East Pass of Choctawhatchee Bay near Destin, Fla, where biweekly or monthly observations were made between June 1968 and December 1970. Others were collected from St. Andrew Bay near Panama City, from Apalachicola Bay, and from Alligator Harbor, Fla. A

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few were taken short distances offshore from these locations.

Numerous field observations were made while diving, and small groups of specimens (2-3) were maintained and casually observed for a few months in 20-gal aquaria.

Eighty-seven specimens were examined for gonad development. Most were examined superficially using a low-power (10-30×) dissecting microscope, and the stage of development of the ovarian portion of the gonad was estimated, following the definitions of Smith (1965) and Moe (1969). Sexual maturity (the presence of Stage 4 oocytes) was determined on the basis of ovarian tissue only, since very small individuals often contained some mature sperm, even though the ovarian tissue was immature. For 22 specimens the gonads were removed, embedded in paraffin, and sectioned. Most specimens had been originally preserved in 10% Formalin[2] and then transferred to 40% isopropyl alcohol. Gonads to be sectioned were removed from the fish, placed in Bouin's fluid for several days, dehydrated in ethyl alcohol, celloidin-methyl salicylate, and xylene, and then embedded in paraffin. Gonads were sectioned at 10 μ, mounted on microscope slides, and stained. Mallory-Heidenhain stain was used for most slides. This stain was easy to use and yielded good contrast between various tissues within the gonad.

Stomachs of 31 specimens were removed and their contents examined under a low-power dissecting microscope. Food items were identified to major group (usually class or order) and counted. The importance of each group was determined by calculating its frequency based upon the total number of food items counted and upon the number of fish containing each food type.

DISTRIBUTION

Briggs (1958) gave the range of *Serraniculus pumilio* as North Carolina to Florida, and the southwestern Gulf of Mexico in shore areas. Subsequent references (Bullis and Thompson, 1965; Cervigon, 1966) indicate that it occurs along the coast of the western Atlantic Ocean from North Carolina to Guyana. Most collections have come from the Atlantic coast of the southeastern United States and from the eastern Gulf of Mexico as a result of the numerous fisheries surveys in these areas (Reid, 1954; Springer and Bullis, 1956; Springer and Woodburn, 1960; Moe and Martin, 1965; Moe et al., 1966; Starck, 1968; Struhsaker, 1969). The species has also been collected in the western Gulf of Mexico off Texas (Ginsburg, 1952; Hildebrand, 1954) and in Campeche Bay off Mexico (Hildebrand, 1955). More recent collecting by the RV *Oregon* and RV *Pillsbury* off the coast of Colombia indicates that the species is also common in the Caribbean Sea (C. R. Robins, pers. comm.). Two specimens have been taken by the *Pillsbury* from off the coast of Honduras.

Serraniculus is unrecorded from the Bahamas (Böhlke and Chaplin, 1968) and apparently also absent from the other islands of the West Indies. Numerous species of fishes have similar continental distributions in the western Atlantic, while other species are restricted to the coral reef areas of the islands and portions of the Central and South American coast where the continental shelf is narrow. The factors which prevent the distribution of continental species in the islands are not completely understood, but probably include differing ecological conditions, as well as competition from closely related and better adapted island species (Robins, 1971). Physical barriers are undoubtedly not important since many of the species have pelagic larval stages, and some free-swimming species such as *Scomberomorus maculatus* are also absent from most of the West Indies. Ecological parameters which may be important are temperature, bottom type, salinity, and turbidity. Temperature may not be important for *Serraniculus pumilio* since it is distributed well into the tropics, but it is apparently more tolerant of low temperatures than are most of the coral reef fishes. *Serraniculus* may prefer continental sediments rather than coral reef debris, but accurate descriptions of substrates where it has been collected are unavailable. In general, the continental species, including *S. pumilio*, are more tolerant of vary-

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

ing conditions, but whether they require such changes is unknown. For species such as *S. pumilio*, which are territorial, competition by other species with similar habitat requirements may be important. Two potential competitors of *S. pumilio* are noted in the following section.

HABITAT

Serraniculus pumilio apparently occurs typically at moderate depths (10-70 m) over the continental shelf but may occasionally occur in shallow coastal waters less than 1 m deep. It has been recorded as deep as 117 m (Bullis and Thompson, 1965).

During this study, the species was often common in the shallow waters along the jetties at East Pass of Choctawhatchee Bay in depths of about 1-10 m but was usually absent during January and February. Inshore populations of *Serraniculus* apparently move offshore to deeper water during the winter. The lowest temperatures at which the species was recorded at East Pass were 13°-14°C. Shallowwater temperatures in the northern Gulf often drop below 10°C during the winter, while the temperature in water deeper than about 18 m usually remains above about 15°C. The minimum temperature extreme at which *S. pumilio* can survive may be about 13°C.

Like other small serranids, this species is most common over sand or shell bottoms near irregularities such as coral or rock outcrops. Springer and Woodburn (1960) noted that it was similar in this respect to *Centropristis ocyurus*, another species restricted to the continental shelf. *Serranus tigrinus* and *S. baldwini* (Robins and Starck, 1961) also occupy such habitats at about the same depth range as *Serraniculus pumilio*, but these two species are restricted primarily to coral reef areas of the West Indies where *Serraniculus* is not found.

A few specimens of *Serraniculus* have been collected in grass beds (mostly *Thalassia* and *Syringodium*) at the mouth of Alligator Harbor. However, in such areas, numerous bare patches of sand bottom are present, and there are accumulations of shell debris in places which provide suitable habitat for the species.

Apparently *Serraniculus pumilio* does not have a particularly restricted home range. The number of individuals observed on the East Pass jetties varied considerably, indicating that individuals were often moving into and out of the area. These observations were based upon adults or advanced juveniles; hence recruitment of populations on the jetties resulted from movement of adults, not from the immigration of recently spawned young. The pattern of movement of adults is not known, but more stable populations may occur on the numerous limestone reefs which lie short distances offshore in the area. Accumulations of mollusk shells occur over most of the sandy bottom in the area and small fishes such as *Serraniculus* could use such accumulations for shelter when moving over open bottoms. In this way *Serraniculus* could easily move the few miles from the offshore reefs to the jetties.

BEHAVIOR

Springer and Woodburn (1960) described *Serraniculus pumilio* as sedentary, but individuals apparently move about considerably. The fish rests on the bottom using its pelvic fins as props and moves about in short "hops" over the bottom. It appears to be territorial and protects its temporary abode (near a large shell, rock, or coral ledge) from intrusion by other fishes. The size of the area defended is not known, but when two or more individuals were placed in a 20-gal aquarium, one became dominant and forced the other fish to remain off the bottom, even when several rock piles were provided as hiding places.

During agonistic displays, *Serraniculus* spreads its dorsal and caudal fins and gill covers, and presents the lateral side of the body to the opponent (Figure 1). During these displays, the dark and light bands on the side of the body become more distinct and series of small, pale spots are clearly visible along the rays of the dorsal and caudal fins. These displays are followed by the fish beating the side of its opponent with its caudal fin and the posterior part of its body. When one individual proves subordinate, it retreats with its dorsal fin depressed and usu-

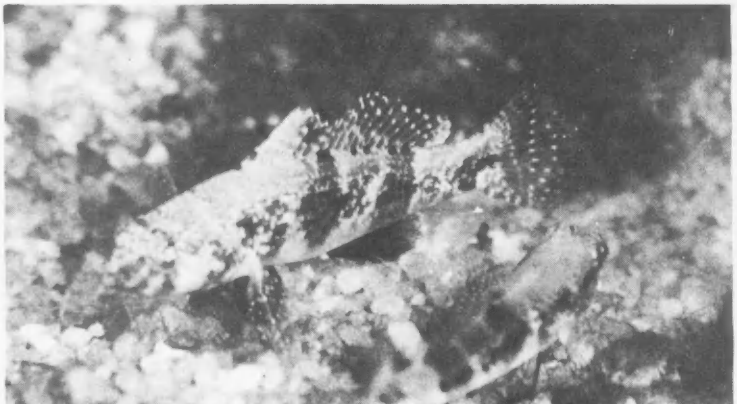

FIGURE 1.—Agonistic display of aquarium-held *Serraniculus pumilio.*

ally with the victor in pursuit. Quite similar agonistic behavior involving fin-spreading and tail-beating has been described in *Serranus scriba* (Kirchshofer, 1954). Subsequently, the subordinate individuals in an aquarium remained in precarious positions in the corners of the aquarium some distance above the bottom. When these fish left such positions, except during periods of feeding, they were soon attacked by the dominant individual and returned to their "sanctuaries" near the surface of the water.

Once, agonistic behavior was observed between two fish on the East Pass jetties, but in this case the retreating individual had its dorsal fin greatly expanded.

REPRODUCTION AND DEVELOPMENT

Microscopic examination of sectioned gonads (Figure 2) proves that *Serraniculus pumilio* is a synchronous hermaphrodite, as Ginsburg (1952) originally supposed. His statement that the testicular tissue is "interspersed with the masses of ripe roe" is misleading, however. The gonads of *Serraniculus* are identical to those of *Serranus* in that the testicular portion is well separated from the ovarian tissue and is restricted to narrow bands which lie along the ventral surface of each gonad (Reinboth, 1962; Smith, 1965).

The smallest and the largest specimens examined had both ovarian and testicular tissue in the gonad and many were seen with both mature eggs and sperm present. As with *Serranus,* internal self-fertilization is undoubtedly impossible since separate ducts are present to carry eggs and sperm. Clark (1959, 1965) found that under aquarium conditions, *Serranus subligarius* could fertilize its own eggs, but mates with another individual and exchanges gametes under normal conditions. Reinboth (1962) also induced self-fertilization in *Serranus scriba* but suggested that paired spawning normally occurs. The same is probably true for *Serraniculus.*

On 10 May 1968, several pairs of *Serraniculus pumilio* apparently involved in reproductive behavior were seen on the sand bottom at the base of the St. Andrew Bay jetties, on the Gulf side of the west jetty in water about 2 m deep. The water temperature was 23°C. Pairs would move slowly about in close proximity with one individual following behind the other. The trailing individual would repeatedly nudge the anal region of its mate. Clark (1959) noted such nudg-

ing behavior in spawning *Serranus*. Although no spawning clasps were observed, six specimens were collected, and subsequent examination revealed that all had large numbers of ovulated eggs within the lumen of their gonads. These specimens were 41.7-48.6 mm SL.

Based upon examination of gonads of preserved specimens, *Serraniculus pumilio* spawns between March and August or September. The number of small individuals collected during these months is limited, so the size at which maturity of the ovarian tissue is reached was not determined. There is some indication that it may be about 40 mm SL. Seven specimens (34.1-41.2 mm) collected in March were immature, while two (43.0 and 44.2 mm) were mature. One specimen (36.6 mm) collected in April had mostly immature gonads but had a few Stage 4 oocytes. Twelve specimens (40.6-49.5 mm) collected in May were mature, while two (40.5 and 40.8 mm) were mostly immature, with only a few Stage 4 oocytes. A few individuals as small as 23 mm SL contained mature sperm, even though the ovarian tissue was immature, but it is not known whether such individuals could successfully spawn as males. Reinboth (1962) noted a similar condition in *Serranus scriba* and *S. cabrilla*, in which the testicular portion of the gonads matured earlier in the annual reproductive cycle and also at a smaller size. He speculated that *S. scriba* in their first year of sexual maturity (120-140 mm body length) function only as males and that the ovarian tissue matures only in fish over 160 mm in length. He did not demonstrate actual spawning in such first-year males, however.

All 38 specimens (15.8-48.8 mm SL) collected in February, September, October, November, and December had immature gonads, although one specimen (42.7 mm) collected in October had a few mature oocytes in the posterior region of its gonad. All specimens larger than 43.0 mm collected from March through August had mature gonads. Specimens with ovulated eggs were collected in May, June, and July.

Nothing is known of the embryonic and larval development of *Serraniculus pumilio*. The eggs of *Serranus* are buoyant (Clark, 1959) and eggs and larvae of *Epinephelus* (family Serranidae) are pelagic (Moe, 1969), but it is not known if the same condition exists in *Serraniculus*. The smallest individual collected during this study (15.8 mm SL) has the general body shape and pigmentation of adults.

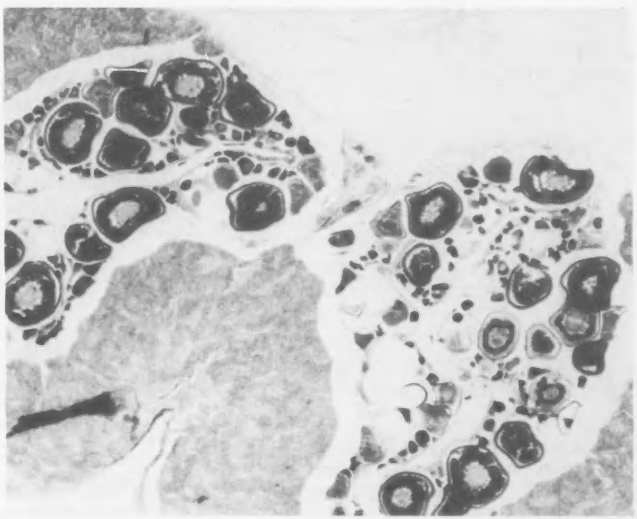

FIGURE 2.—Cross section through the basal (posterior) portion of the gonads of *Serraniculus pumilio* showing mature ovarian and testicular tissues.

GROWTH

A length-frequency distribution (Figure 3) of *S. pumilio* occurring in inshore waters indicates that all belong to the same year class and that no second year fish occur inshore. Small fish which were apparently spawned in the summer appear inshore in September, and some may remain throughout the winter. Most probably move to deeper water as the temperature drops and move inshore again in March. No adults were found after August. The largest specimen collected during this study (54.1 mm) is considerably smaller than the maximum size attained (80 mm SL—Ginsburg, 1952) so possibly the larger, second year fish remain offshore in deeper water.

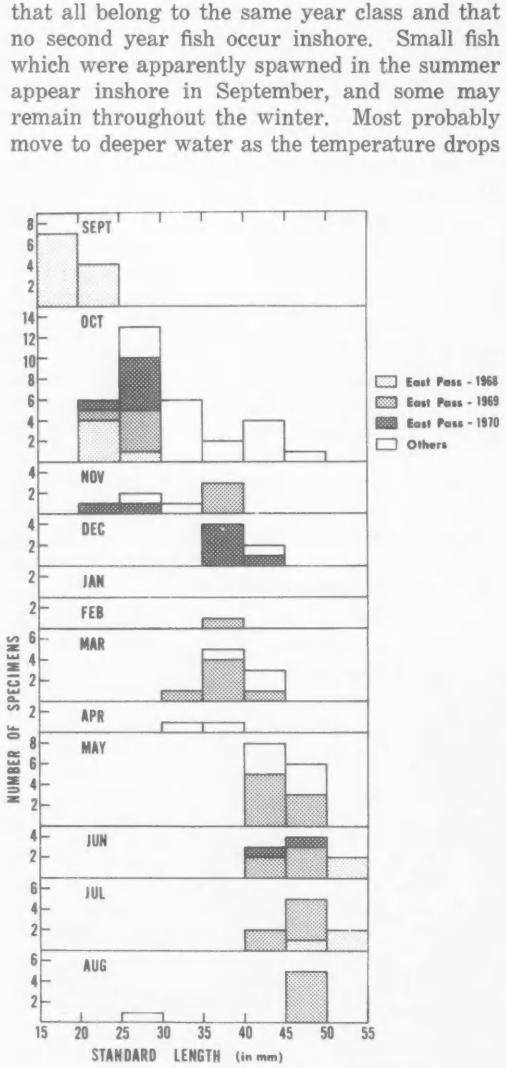

FIGURE 3.—Monthly length-frequency distributions of *Serraniculus pumilio* collected inshore at East Pass, Choctawhatchee Bay, Fla., and at other locations in the northern Gulf of Mexico.

FOOD HABITS AND PREDATION

Thirty-one specimens were examined for stomach contents, but two were empty. Results of stomach analyses are shown in Table 1. *S. pumilio* feeds predominantly upon crustaceans, which made up 91% of the total number of food items. Numerically, amphipods are the most common group, but shrimps and crabs comprise a larger volume of the stomach contents when present and may be the most important food items. *Serraniculus* appears to be an indiscriminate carnivore, feeding upon any small organism which it discovers, but showing preference for small crustaceans.

The extent of predation by other fishes on *S. pumilio* is not known. It seems strange that D. S. Jordan never found this species in his extensive studies of the stomach contents of snappers and groupers taken in the northern Gulf of Mexico (Jordan, 1884, 1886; Jordan and Gilbert, 1882, 1883; Jordan and Swain, 1885). Stephen A. Bortone (personal communication) found one specimen in the stomach of a *Lagodon rhomboides* collected in Apalachee Bay, 11 October 1969, about 2 miles south of the St. Marks lighthouse, Wakulla County, Fla., at a depth of about 3 m. The general cryptic coloration and sedentary habits of the pygmy sea bass may conceal it from most predators.

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TABLE 1.—Food habits of *Serraniculus pumilio* based on stomach analysis of 29 specimens (15.8-54.1 mm SL) collected in inshore waters of the northern Gulf of Mexico, 1968-71.

Food types	Number of items	Percent of total number	Number of fish containing each	Percent frequency of occurrence
Crustacea	262	91.0	28	96.5
Amphipods	110	38.2	17	58.6
Caprellid amphipods	12	4.2	6	20.7
Isopods	32	11.1	8	27.6
Copepods	20	6.9	7	24.1
Tanaidaceans	4	1.4	3	10.3
Cumaceans	1	0.3	1	3.4
Shrimps (adults)	18	6.2	10	34.5
Shrimp zoea (?)	23	8.0	7	24.1
Crabs (adults)	21	7.3	9	31.0
Crab megalops	14	4.9	2	6.9
Unidentified crustacean	7	2.4	5	17.2
Polychaetes	9	3.1	9	31.0
Unidentified wormlike organisms	13	4.5	1	3.4
Gastropods	1	0.3	1	3.4
Algae	(1 mass)	0.3	1	3.4
Fishes	2	0.7	2	6.9

Dr. Camm C. Swift and Stephen A. Bortone, both formerly of Florida State University. I also thank Dr. P. P. Graziadei of Florida State University who allowed me to use facilities in his histology laboratory in preparing microscope slides of sectioned gonads. I greatly appreciate the comments of Dr. C. Richard Robins of the Rosenstiel School of Marine and Atmospheric Science at the University of Miami (Florida) and his critical review of this manuscript. Special thanks are expressed to Dr. Ralph W. Yerger of Florida State University for his continued encouragement in my studies of marine fishes of the northern Gulf of Mexico and for reviewing and editing the original manuscript. I am indebted to my wife, Diana, for her encouragement and patience and for her assistance in typing.

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DESIGN AND EVALUATION OF A SAMPLER FOR MEASURING THE NEAR-BOTTOM VERTICAL DISTRIBUTION OF PINK SHRIMP, *PANDALUS JORDANI*

ALAN J. BEARDSLEY[1]

ABSTRACT

A shrimp sampler was constructed as one portion of a research effort dealing with the development of a fish-shrimp separator trawl. The sampler segregated shrimp caught in a series of 1-ft high vertical openings positioned between the seabed and a height of 13 ft above the seabed. Knowledge of the vertical distribution of shrimp was considered essential in the design of an efficient shrimp trawl. Results indicated that vertical distributions of shrimp vary, and the amount of light striking the seabed is suggested as the triggering stimulus. Auxiliary investigations conducted with the sampler dealt with evaluations of mesh size and tickler chain. Experiments indicated that mesh sizes smaller than 2 inches restrict the passage of shrimp. The weight of shrimp caught was nearly doubled when a tickler chain was used. The sampler may have application to both shrimp biologists and commercial fishermen.

Research was begun in our laboratory on trawls capable of separating pink shrimp, *Pandalus jordani*, from other marine organisms and debris while the net is being towed over the seabed (High, Ellis, and Lusz, 1969; Beardsley and High, 1970). Knowledge of the near-bottom vertical distribution of shrimp was considered essential to the design of an effective shrimp trawl since the vertical height of any bottom trawl should approximate the off-bottom distribution of the target species.

Subsequently a multipurpose shrimp sampler was designed to facilitate investigation of shrimp distributions above the seabed by 1-ft intervals. Auxiliary investigations conducted with the sampler included evaluating the effects of: (1) diel or circadian movements on the abundance of shrimp near the seabed; (2) light on shrimp vertical distribution; (3) mesh size on the retention of shrimp and other marine organisms; and (4) a tickler chain on shrimp catch rate and vertical distribution.

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METHODS AND MATERIALS

The shrimp sampler was designed for towing on the seabed either attached in the mouth of a conventional 57-ft Gulf shrimp trawl or directly to dandy lines without the net. All data presented in this paper resulted from tows without an attached net. This fishing configuration made the sampler easier to set and retrieve; it also eliminated the variability in shrimp catches caused by differences in fishing modes. Commercial trawling conditions were simulated using 5- × 7-ft otterboards, 15-fm dandy lines, and a towing speed of 2½ knots.

The shrimp vertical distribution sampler (Figure 1) consists of an aluminum frame partitioned into 18 openings each measuring 1 ft vertically by 2 ft horizontally. The sampler openings are positioned in six horizontal rows (1 ft high) and three vertical columns (2 ft wide), resulting in a triplicate series of vertical samples. A vertical extension was bolted with ⅜-inch bolts behind the sampler, permitting sampling as high as 12 to 13 ft above the seabed.

Individual collector bags of ¾-inch mesh[2] were lashed behind the sampler, thereby segregating and retaining the shrimp that entered the separate sampler openings. The dandy lines were attached to the sampler at the four center pad eyes and led freely through shackles at the four corner pad eyes. This method of attachment distributed the pull of the dandy lines across the face of the sampler in the event it hit a heavy object during a tow. Aluminum trawl floats (8-inch diameter) buoyed the sampler upright during setting and retrieving, whereas water pressure maintained this posture while towing.

During tickler chain (a device used to stimulate shrimp off of the seabed and into the trawl) evaluations, the chain was attached directly to the lower dandy lines with cable clamps and shackles. The length of chain was adjusted so it maintained a position 2½ ft in front of the bottom center of the sampler as determined by scuba diver observations.

Several mesh sizes[3] were evaluated using rectangular aluminum frames (separator panels) placed over the sampler openings (Figure 1). Aluminum teeth separated the panels on the front of the sampler. Although each frame had mesh of uniform size, the mesh size between frames varied between 1¼ and 3 inches. Comparisons of different mesh sizes were facilitated by placing the meshes to be compared on the lateral two columns of vertical openings on the sampler. Two-inch mesh webbing was placed over the center column of the sampler during mesh size comparisons so this column could act as a gross index of relative shrimp abundance on the fishing grounds. The tow direction was reversed after each tow, and the lateral two panels were exchanged on alternate tows to reduce any difference in catch efficiency by one side of the sampler or the other.

During fishing trials on shrimp beds off the Washington coast, adequate sample sizes (50-2,000 g of shrimp per collector bag) were obtained from tows of 10-min duration without separator panels and 15 min with separator panels.

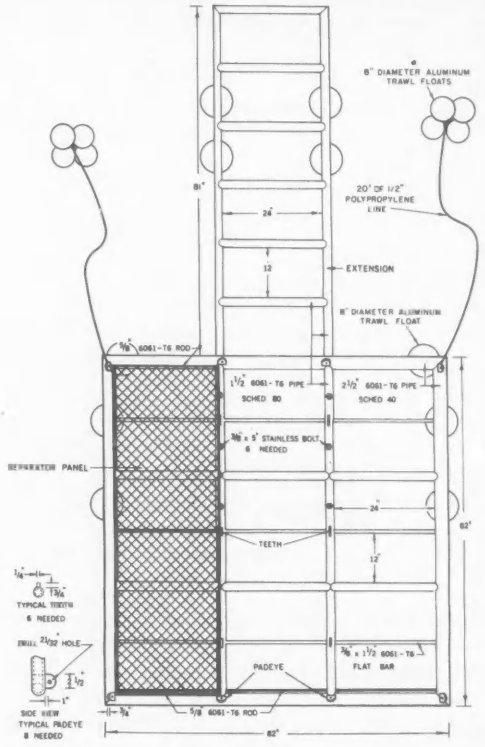

FIGURE 1.—Construction specifications for the shrimp sampler and extension.

The individual collector bags were emptied at the conclusion of each tow and the contents labeled and frozen. In the laboratory shrimp were thawed and the weight, the carapace length (base of eyestalk to the dorsal posterior margin of the carapace), and sex recorded.

PRELIMINARY EVALUATIONS OF THE SAMPLER

Scientist-divers first appraised the shrimp sampler in Puget Sound as it was being towed on bottom in 8 fm of water at 2½ knots. On each of eight tows the sampler was reported to

[2] All mesh sizes in this paper are stretched measure.
[3] The following mesh and thread sizes and materials were evaluated: 1¼-inch mesh, 9 thread, nylon and acetate; 1½-inch mesh, 15 thread, nylon; 1¾-inch mesh, 18 thread, nylon; 2-inch mesh, 12 thread, nylon; 2½-inch mesh, 21 thread, nylon; 3-inch mesh, 18 thread, nylon.

be upright, stable, less than 3 inches off the seabed, and perpendicular to the direction of tow.

Fishing trials were then conducted on populations of pink shrimp and spot shrimp, *Pandalus platyceros*, in 40-60 fm of water in Dabob Bay, Wash. Most shrimp were taken near the seabed (Figure 2), but substantial numbers of pink shrimp were taken as high as 5 to 6 ft off bottom, whereas no spot shrimp were found higher than 3 to 4 ft. This phenomenon was interpreted as a behavioral difference between the two species rather than a difference due to physical size as one might expect the larger spot shrimp to jump higher off the seabed.

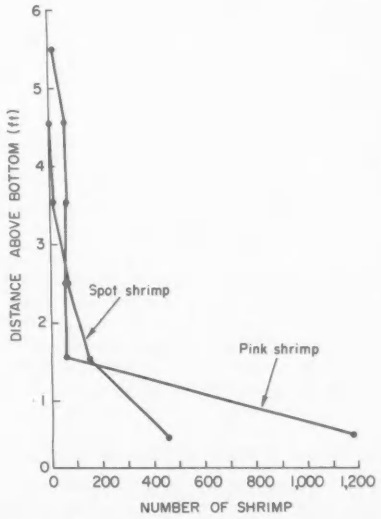

FIGURE 2.—Vertical distribution of pink and spot shrimp taken in four tows in Dabob Bay, Wash. Numbers of shrimp are totals for the 1-ft intervals.

Subsequent fishing trials with the shrimp sampler were conducted on pink shrimp beds of commercial importance off Grays Harbor, Wash. A total of nine tows were made without separator panels and nine with 2-inch mesh across the front of the sampler. Total weights and carapace lengths for shrimp in all sampler openings in each of the vertical columns for each fishing mode were pooled (54 samples). The means for these data are presented in Table 1.

These data were further analyzed using a three-way factorial analysis of variance with the three main effects being vertical columns and horizontal rows of the sampler and repetitive tows (Table 1). In tows without separator panels the weights of shrimp in vertical columns were significantly different ($F = 3.24$), but a comparison of starboard and port vertical columns revealed their difference was not significant ($F = 0.430$) at the 5% significance level. The average of starboard and port colmns for shrimp weight was significantly different from weights for the center column ($F = 6.06$). Analysis of the data for carapace length of shrimp without separator panels and for both shrimp weight and carapace length with 2-inch separator panels indicated no significant difference

TABLE 1.—Comparison of pink shrimp caught with and without 2-inch mesh separator panels on the front of the shrimp vertical distribution sampler. Means and F values were computed from 54 samples (i.e., six vertical openings over a nine-tow repetition).

Type of comparison	Degrees of freedom	Critical F value at 5% significance level	Without panels		With 2-inch panels	
			Weight	Length	Weight	Length
Mean[1]						
Starboard column			178.0	18.2	81.2	18.1
Middle column			156.0	17.9	83.3	17.8
Port column			172.0	18.3	86.6	19.9
F value						
All vertical columns	2,80	3.11	3.24	[2]1.20	[2]0.529	[2]0.699
Middle vs. ½(starboard + port)	1,80	3.96	6.06	[2]2.32	[2]0.017	[2]0.831
Starboard vs. port	1,80	3.96	[2]0.430	[2]0.074	[2]1.04	[2]0.56
Horizontal rows	5,80	2.33	10.4	6.28	4.65	3.78
Repetitive tows	8,80	2.05	52.0	5.81	15.0	4.71

[1] Weight in grams; length in millimeters.
[2] Not significantly different at 5% significance level.

between vertical columns. Since the differences in shrimp catches between port and starboard vertical columns were not significant during tows either with or without separator panels, later comparisons of the effect of mesh size on shrimp catches were made between the starboard and port vertical columns.

As might be expected, significant differences were evident for both horizontal rows on the sampler and repetitive tows. The differences in shrimp vertical distribution (horizontal rows) are discussed later in the paper. Differences in catch during repetitive tows were anticipated as shrimp samples were collected over several months on several shrimp beds.

DAYTIME VERTICAL DISTRIBUTION OF SHRIMP

In March 1969 a series of eight tows were made with the shrimp sampler in 71 fm off Destruction Island, Wash. Principal objectives were to determine if differences in number and size composition of shrimp would occur with increasing height off bottom. Four hauls were made without separator panels and four hauls with uniform 2-inch mesh across the front of the sampler. The greatest number of unmarketable (less than 15-mm carapace length) and marketable (15-mm carapace length or greater) shrimp were taken in sampler openings near the seabed. The ratio of marketable to unmarketable (pinhead) shrimp increased with distance off bottom (Figures 3 and 4). The relationship between distance off bottom and length-frequency of shrimp is shown in Figure 5 for the same series of tows. This figure indicates that shrimp were most abundant near the seabed and a high percentage were small.

Additional tows with the sampler under a variety of conditions (weather, time of day, season)

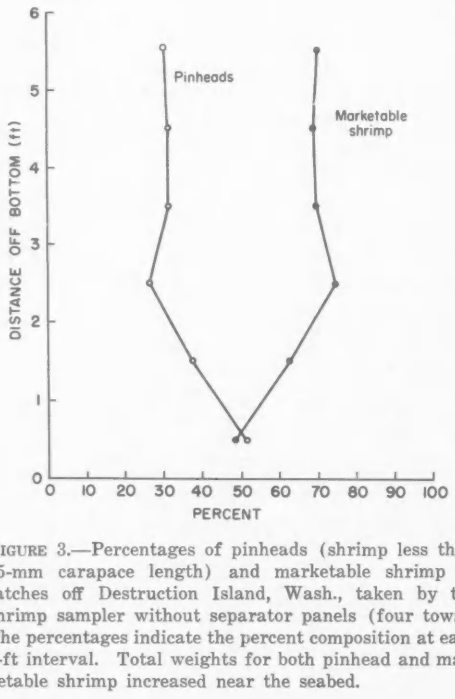

FIGURE 3.—Percentages of pinheads (shrimp less than 15-mm carapace length) and marketable shrimp in catches off Destruction Island, Wash., taken by the shrimp sampler without separator panels (four tows). The percentages indicate the percent composition at each 1-ft interval. Total weights for both pinhead and marketable shrimp increased near the seabed.

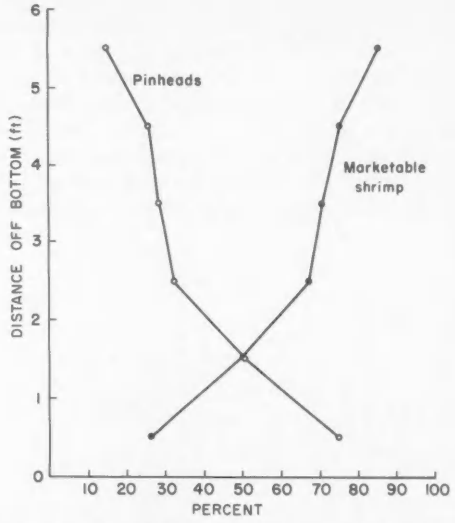

FIGURE 4.—Percentages of pinheads (shrimp less than 15-mm carapace length) and marketable shrimp in catches off Destruction Island, Wash., taken in four tows of the shrimp sampler with separator panels. The percentages indicate the percent composition at each 1-ft interval. Total weights for both pinhead and marketable shrimp increased near the seabed.

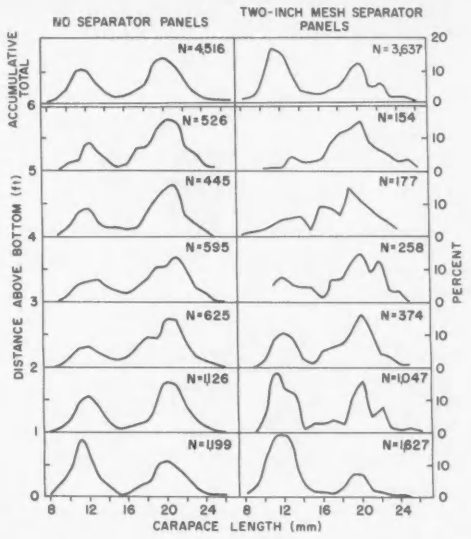

FIGURE 5.—Relation of length frequency of shrimp to distance off bottom for shrimp sampler tows off Destruction Island, Wash. Four tows were made with no separator panels and four with 2-inch separator panels. N is the total number of shrimp taken in the sampler openings with the cumulative totals for four tows shown at the top of the figure.

indicated the vertical distribution of shrimp is not static but subject to dynamic changes, often in a brief period of time. Representative midmorning tows for three different days are presented in Figure 6. Widely divergent shrimp distributions are evident in this figure. The most rapid alteration in shrimp distribution was observed between midmorning tows on 22 and 23 June (Figure 6). Over the same time period the weather changed from partly cloudy to complete overcast with rain. Commercial shrimp fishermen trawling on the same shrimp grounds reported a reduction in shrimp catches accompanying the change in cloud cover. As commercial shrimpers drag their trawls on bottom regardless of weather, it is conceivable that their nets were passing under large numbers of shrimp. During sunny weather with relatively clear water, shrimp were found concentrated near the seabed as on 9 August in Figure 6.

DIEL MOVEMENTS OF SHRIMP

Diel variations in shrimp distribution were investigated with the sampler during three day-night cycles using the shrimp sampler. All tows were 15 min in length and were made with 2-inch separator panels on the sampler. During any single diel cycle, all tows were made in the same direction and in the same location as indicated by the vessel's compass, depth sounder, and loran.

Vertical distributions for pink shrimp collected during three diel cycles are presented in Figure 7. Tows on 24 March were conducted under a cloudless sky with the greatest quantity of shrimp taken early in the day. Greatly reduced catches were taken at night. In general, shrimp appeared to be higher above the seabed during early morning and evening tows.

The weather preceeding 28 March was overcast with rain. Tows during 28 March (Figure 7) indicated shrimp were not plentiful near the

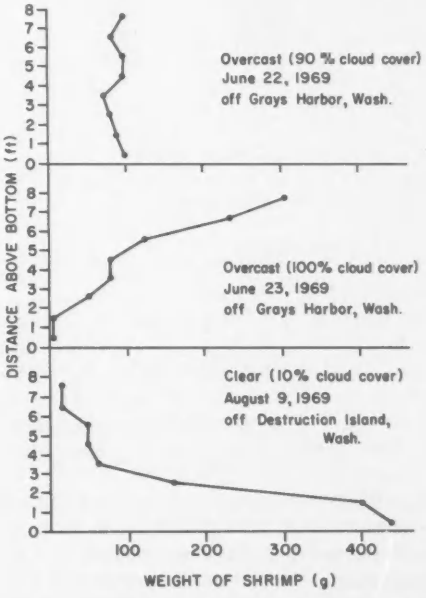

FIGURE 6.—Examples of three widely divergent shrimp vertical distribution patterns in the shrimp sampler on three different tows.

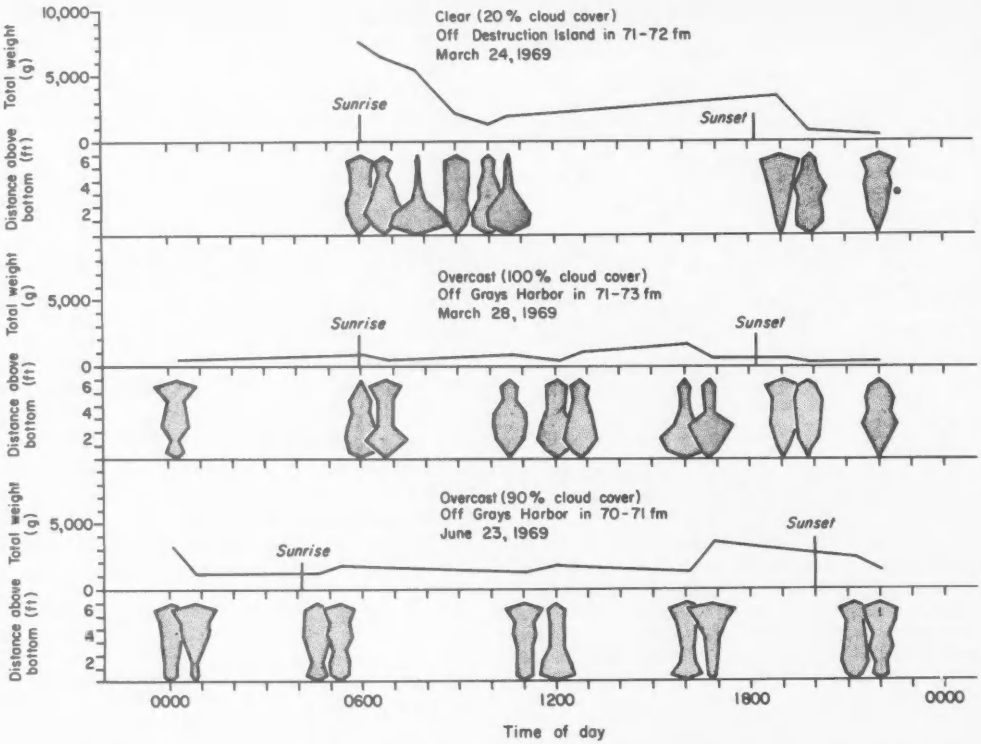

FIGURE 7.—Three different diel distributions of pink shrimp collected with the shrimp sampler. The varying width of each diagram represents the percentage proportion of the catch taken at various distances from the bottom of the sampler.

seabed. The greatest quantity of shrimp were taken during the day.

The tows on 23 June presented a valuable opportunity to observe the changes in shrimp vertical distribution accompanying a change in cloud cover. The 2 days preceeding 23 June were sunny. Tows with the shrimp sampler on these days indicated shrimp were concentrated near the seabed during daylight hours. Commercial fishermen working near the sample station were making good catches of shrimp.

On the evening of 23 June a zone of low barometric pressure moved into the area with resulting cloud cover and rain squalls on 23 June. Catches by commercial fishermen dropped to a fraction of those taken on previous days. The vertical distribution sampler indicated shrimp were well off bottom (Figure 7) with reduced shrimp abundance, compared with tows made on previous days. A most interesting situation occurred during tows made in twilight and after dark as the catch rates were much higher than in tows made in the preceeding daylight hours.

MESH SIZE EVALUATIONS

The effect of mesh size on the movement of shrimp was investigated by placing web of two different sizes on separator panels over the port and starboard vertical columns. A total of six different mesh sizes were evaluated in this manner. Two-inch mesh was placed over the center

TABLE 2.—Comparison of pink shrimp caught behind separator panels of differing mesh size. Means and F values were computed from 24 samples (i.e., six vertical openings over a four-tow repetition).

Item				F value		
				All vertical columns[1]	Middle vs. ½(starboard + port)[2]	Port vs. starboard[2]
Mesh size (inches)	1.0	2.0	1.5			
Mean weight of shrimp (g)	27.6	329.3	112.7	190.0	202.0	16.3
Mean length of shrimp (mm)	14.7	16.9	17.6	13.2	[3]2.03	24.3
Mesh size (inches)	1.75	2.0	2.0			
Mean weight of shrimp (g)	166.8	225.7	243.7	11.4	[3]1.98	20.9
Mean length of shrimp (mm)	19.1	19.1	19.2	[3]0.605	[3]0.330	[3]0.870
Mesh size (inches)	2.5	2.0	3.0			
Mean weight of shrimp (g)	231.3	222.0	260.7	9.67	[3]2.60	4.71
Mean length of shrimp (mm)	19.4	19.3	19.2	[3]0.948	[3]0.013	[3]1.88

[1] The F value at the 5% significance level is 3.32 with 2 and 30 degrees of freedom.
[2] The F value at the 5% significance level is 4.17 with 1 and 30 degrees of freedom.
[3] Not significantly different at 5% significance level.

vertical column as a control or index of the relative abundance of shrimp available.[4] The positions of the separator panels being evaluated (port and starboard) were switched after each set of two tows, and tow direction was altered 180° after each haul. This was done to reduce any sampling bias attributable to one side of the sampler or the other. Two different mesh sizes were compared over four consecutive tows.

The relationship between mesh size and the catch of shrimp as determined by tows with the shrimp sampler is shown in Table 2. The mean sample weight of shrimp catches increased directly with the mesh size, but the rate of increase diminished in mesh sizes above 2 inches. Differences between the total weight of catches taken with 2½-inch mesh and 3-inch mesh were significant ($F = 4.71$), but difference in the mean weights (231.3 and 260.7 g) for these mesh sizes was less than the differences between the means for 1-inch and 1½-inch mesh (27.6 and 112.7 g) and for 1¾-inch and 2-inch mesh (166.8 and 243.7 g). These differences are also suggested by the computed F values in Table 2. Figure 8 shows this relation between mesh size and catch from the data in Table 2. In this figure mean weight and carapace length (means) of shrimp catches for the six different mesh sizes have been converted into a percentage of the weight and length (means) taken by the center vertical column (control) with its standard 2-inch mesh separator panel.

In contrast, the mean carapace length of shrimp did not differ significantly with increasing mesh sizes above 1½ inches (Table 2 and Figure 8). This indicates that the larger shrimp are able to pass readily through the 1½-inch mesh if the meshes are open and held at right angles to the current. Meshes in the intermediate and cod end of conventional west coast shrimp trawls are 1½- to 1⅝-inch mesh. However, shrimp do not pass through these meshes in large quantities because the meshes are normally partially closed and nearly parallel with the current (High et al., 1969).

EFFECT OF TICKLER CHAIN ON SHRIMP CATCHES

Commercial shrimp fishermen in the northeastern Pacific commonly employ a contrivance called a "tickler chain" to excite shrimp off bottom in an effort to increase their catches. This chain is several feet shorter than the trawl footrope with the ends attached to the ends of the foot rope. In this configuration the tickler chain

[4] In the situation where small mesh sizes (i.e., 1¼ and 1½ inches) were being compared on the lateral vertical openings of the sampler, there is the possibility that shrimp catches in the center vertical opening (2-inch mesh) would be proportionally greater than when larger mesh sizes (i.e., 2½ and 3 inches) were being compared. The likelihood of shrimp avoiding the small mesh was considered remote on the basis of diver observations of fish pinned against the web in the separator panels and the presence of large numbers of gilled shrimp in small-mesh web on the separator panels at the conclusion of a tow.

TABLE 3.—Shrimp catches with and without a tickler chain attached to the shrimp vertical distribution sampler.

Location	Date	Time	Depth (fm)	Shrimp catch (g)	
				Without tickler chain	With tickler chain
Off Grays Harbor, Wash.	6-23-69	1150-1205	73	2,270	
		1256-1311	73		4,561
		1345-1400	73	3,208	
		1425-1440	73		8,198
		1515-1530	73	3,696	
		1610-1625	73		4,081
Off Destruction Island, Wash.	6-24-69	0915-0930	76	221	
		0958-1012	76		889
		1040-1055	76	4,064	
		1125-1140	76		1,276
	8-29-69	0655-0710	66	3,376	
		0820-0835	66		9,983
		0915-0930	66	3,451	
		1000-1015	66		8,900
	11-13-69	0908-0918	69	1,887	
		1000-1015	69		5,364
		1103-1118	69	1,942	
		1232-1247	69		3,906
		1327-1342	69	1,230	
		1415-1430	69		912
		1508-1523	69	1,569	
		1605-1620	69		3,574
			Total	26,914	51,644

precedes the footrope as the net is being towed on bottom. Even though the tickler chain is accepted and used by most shrimp fishermen under the assumption that it increases catches, very little is known about the effect of this chain on either the quantity of shrimp caught or the vertical distribution of shrimp as they enter the trawl.

Utilizing the unique features of the shrimp sampler, a brief examination of the effects of tickler chain on shrimp height distribution was undertaken. Unwanted fish and debris were eliminated from the shrimp catches by placing 2½-inch mesh webbing on separator panels over the entire face of the sampler. On alternate tows a length of ⅜-inch tickler chain was placed 2½ ft in front of the bottom of the sampler. All comparative tows were made in the same direction and over the same track line as determined by loran, compass, and depth sounder. Over a 4-month period 22 comparative hauls were made in this manner.

Table 3 shows the catch of shrimp by weight for these tows. Aggregate catches with the tickler chain were nearly twice as great as those without the chain. Summation of the total shrimp weights for each sampler height revealed that when the tickler chain was used, a greater proportion of shrimp were taken in the lower sampler openings in contrast to higher distribution without the chain (Table 4). The effects of a tickler chain on the size distribution of shrimp were also examined. The carapace lengths from shrimp in 200-g samples from each sampler opening were measured. These data indicate that at all distances off the bottom, there

TABLE 4.—Comparison of shrimp catches at various distances off the bottom in the shrimp vertical distribution sampler with (+) or without (−) the tickler chain. These data were computed from the 22 tows presented in Table 3.

Distance off bottom (ft)	Weight (g)			Percent of catch for each height interval	
	−	+	+/−	−	+
1	5,478	15,594	2.8	13.2	30.2
2	6,368	17,064	2.8	11.9	33.0
3	4,859	8,047	1.7	12.8	15.6
4	3,445	4,159	1.2	18.1	8.0
5	3,211	3,375	1.1	23.7	6.5
6	3,555	3,465	1.0	20.3	6.7
			Total	100.0	100.0

was no significant difference between sample means for shrimp carapace lengths in catches made with or without the tickler chain (Table 5).

TABLE 5.—Comparison of mean carapace length of shrimp (computed from 200-g samples) taken in the shrimp vertical distribution sampler with (+) or without (−) the tickler chain. These data were computed from the 22 tows presented in Table 3. The F value at the 10% significance level is 2.79 with 1 and 64 degrees of freedom.

Distance off bottom (ft)	Mean carapace length (mm)		F value
	−	+	
1	16.2	16.7	0.856
2	16.7	17.0	0.616
3	17.1	17.3	0.299
4	17.2	17.6	0.830
5	17.3	17.1	0.092
6	17.5	17.3	0.133

DISCUSSION

Confidence in the shrimp sampler as a research tool capable of indicating the height of shrimp near the seabed resulted from diver observations, trial tows in Dabob Bay, and statistical evaluations of catches made on offshore shrimp grounds. Neither daylight distributions of shrimp off the seabed nor abrupt changes in vertical distributions were expected. The parameters responsible for changes in distribution were not investigated, but other papers (Schaefers and Johnson, 1957; Schaefers and Powell 1958; Alverson, McNeely, and Johnson, 1960; Pearcy, 1970) indicate pink shrimp follow diel or circadian movements which may be triggered by changes in light levels. Similar differences in illumination during daylight hours may be the cause of more subtle alterations in shrimp distribution near the seabed. Tows with the shrimp sampler indicated shrimp were further from the bottom during daytime tows under overcast skies. Commercial fishermen using bottom trawls commonly report reductions in shrimp catches when they encounter turbid water and overcast weather, or both.

This evidence suggests changes in catch rates for pink shrimp are not due entirely to endogenous factors as their distribution appears to change in direct response to light intensity regardless of the time of day. Exogenous rhythmicity in crustaceans has been demonstrated previously by Skud (1968) where during a total eclipse of the sun over Maine in July 1963, crustaceans exhibited a variety of responses from no response to movements toward or away from the surface at totality. Data collected with the shrimp sampler suggest pink shrimp will move off bottom during the day (probably to feed) if the light intensity is reduced enough to present some protection from predators. These movements may also be directly associated with migrations of prey. One explanation for relatively dense concentrations of shrimp near the seabed at night during overcast weather is that these shrimp were able to come off the bottom during the day to feed and returned to the seabed when they became satiated.

The shrimp sampler indicated the highest proportion of small shrimp occur near the seabed. Commercial fishermen could avoid these shrimp by "flying" their nets 2 ft off bottom, but this strategy would also eliminate significant numbers of large shrimp from the catch. Separation and release of small shrimp once they enter the trawl is a difficult if not impossible task. Experiments with the shrimp sampler indicated that the mesh size necessary to segregate shrimp by size is extremely critical even in fully opened meshes at right angles to the current (Figure 8). The problem is compounded in a trawl where few meshes are fully opened and their orientation to the current varies. Moreover large numbers of shrimp are swept in mass into the trawl cod end and may never encounter trawl meshes. These factors reveal the futility of shrimp trawl mesh size restrictions when the design of the trawl is not considered.

Mesh size comparisons indicate that the optimum mesh size for separator panels in shrimp separator trawls should be 2 inches (Figure 8). Smaller mesh would reduce the catch of shrimp, and a larger mesh size would not appreciably increase the size or catch of shrimp captured but could introduce more contaminating organisms into the catch. These results compare favorably with fishing trials of shrimp separator trawls with different mesh sizes in the separator panel. Two-inch separator panels are now standard in this gear.

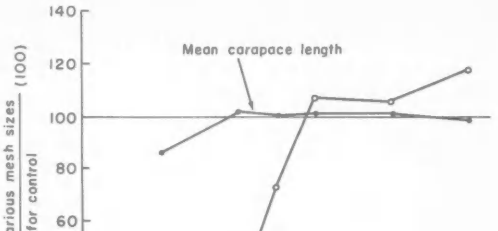

FIGURE 8.—Relationship between mesh size of separator panel and the means of shrimp length and total weight. The values for the mean carapace length and mean sample weight are compared with the shrimp catches (means) taken behind the 2-inch mesh separator panels (control).

The tickler chain caused a significant increase in the number of shrimp entering the lower portion of the shrimp sampler. This phenomenon suggests that the tickler chain either excites shrimp into the water column that normally would pass under the sampler or confuses shrimp so that they are unable to avoid the sampler. The fact that pink shrimp can be readily taken in a plankton sampler with an opening 15 cm in diameter indicates that avoidance may not be an important consideration. The major effect of the tickler chain is probably to move shrimp vertically where they are vulnerable to capture by the trawl.

The utility of the shrimp sampler in describing the vertical distribution of shrimp suggests that it would be a valuable tool for providing supportive evidence necessary for sound management decisions regarding shrimp resources. For example, in California, trawl surveys of the shrimp beds are used to estimate the quantity and quality of shrimp available and hence establish the quota size (Abramson, 1968). These analytical estimations of the standing stock of a shrimp bed are based on the assumption that catch per unit of effort is a function of stock density in the area being surveyed and that changes in catch per effort are directly proportional to changes in density (Ricker, 1958; Gulland, 1964). Equations relating population size to catch per effort for trawl gear (Alverson and Pereyra, 1969) require some knowledge of the vulnerability of shrimp within the influence of the trawl and the proportion of the total shrimp stock in the water column sampled by the trawl. Estimates for vulnerability of shrimp have traditionally been placed near 1 largely because of a lack of knowledge regarding the behavior of shrimp to trawls. With consideration of the size of the trawl opening and the erratic escape movements of shrimp, a vulnerability coefficient of 1 may be relatively accurate. However, use of the shrimp sampler has shown that the coefficient of catchability for a shrimp trawl which is towed a constant distance off bottom may vary dramatically from day to day. Often the catch coefficient would not approach 1 for a trawl having a 4-ft vertical opening. Thus the overall coefficient, which is a product of the vulnerability and catchability coefficient, may at times be considerably less than 1 if shrimp are being sampled with a conventional shrimp trawl. Moreover, the value for the overall coefficient would vary from day to day and reduce the accuracy of population size estimates. The tickler chain must also have an important effect on the vulnerability coefficient, but this relation has not been explored.

The greatest utility of the shrimp sampler in providing estimates of standing stock may be realized when the sampler is towed alternately with a standard trawl. This approach has been taken by scientists at the Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, Alaska (James Olson, pers. comm.) where estimates were being made of the standing stock of shrimp in Kachemak Bay, Alaska. In this instance the sampler was used to determine the catchability coefficient of the standardized shrimp trawl used in the standing stock estimates.

The sampler has also been towed alternately with trawls in an experiment to measure the fishing power of four dissimilar shrimp trawls near Kodiak, Alaska (Lael L. Ronholt, North-

west Fisheries Center, National Marine Fisheries Service, NOAA, Kodiak, Alaska, pers. comm.) Biologists from the Fish Commission of Oregon (Jack G. Robinson, per. comm.) now insert a modified sampler, 2 ft wide by 9 ft tall, in the mouth of a conventional 41-ft Gulf shrimp trawl to achieve estimates of trawl efficiency.

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A REVIEW OF THE CHEMICAL AND NUTRITIVE PROPERTIES OF CONDENSED FISH SOLUBLES

JOSEPH SOARES, JR.,[1] DAVID MILLER,[2] SUSAN CUPPETT,[2] AND PAUL BAUERSFELD, JR.[2]

ABSTRACT

This paper attempts to review some of the pertinent data available on the chemical and nutritive properties of condensed fish solubles with special reference to condensed menhaden solubles. Information concerning other kinds of fish solubles from various published sources is tabulated for comparison. The results of three analytical and three biological studies of menhaden solubles are reported.

Data show that menhaden stickwater contains an average of 4.8% protein, 93.4% water, and about 1.25% lipid. The solids are concentrated about seven times by vacuum evaporation to yield condensed solubles. Data show that this product contains about 32% protein, 49% water, and 11% fat. Additional data are presented on the content of amino acids in fish solubles, which show that the indispensable amino acid tryptophan is relatively low and, on the content of essential inorganic elements which are shown to be present, generally in acceptable levels. Fish solubles are shown to be rich sources of choline, niacin, pantothenic acid, riboflavin, biotin, and vitamin B_{12}.

An experiment with broiler chicks showed that the average metabolizable energy content of 10 samples of condensed menhaden solubles from commercial plants located along the Atlantic and Gulf coasts was 2.03 kcal/g on an "as fed" basis. Average protein and fat digestibility was 89 and 57%, respectively.

Further studies with broiler chicks showed that significant unidentified growth factor responses could be obtained when 5% menhaden solubles was used in diets. A significant response was obtained even when the chicks were reared in a gnotobiotic environment. This indicates that the presence of bacteria is not necessary for solubles to produce a growth response in chicks.

This review attempts to discuss some of the more pertinent recent published and unpublished data available on the chemical and nutritive properties of condensed fish solubles. For many years stickwater was considered as a waste effluent and was not used in animal feeds or in other manufacturing processes. However, with the postwar surge in production of fish meal, this by-product began to be recognized for its nutritional value. In the presynthetic nutrient era, condensed fish solubles was recognized as an outstanding source of B vitamins and minerals for poultry and swine. Later, solubles was the principle source of the "animal protein factor" or vitamin B_{12}. Today we still consider condensed fish solubles to be valuable for these purposes, but now more emphasis is put on its unidentified growth factor content.

There are various sources and kinds of condensed fish solubles available in the United States. However, about 80% of the solubles used in this country are produced by the menhaden reduction industry located along the Atlantic and Gulf coasts. Since 1963, the quantity of solubles available for animal feedstuff supplementation in the United States has averaged about 90,000 tons annually.

However, because of the difficulty in handling, storing, and mixing the viscous condensed fish solubles, a considerable quantity of this product is dehydrated on a carrier to produce a free-flowing dry product. One such product is "full

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meal" containing 1 part condensed solubles to 3.5 parts of fish meal. This recombination of the two fish products is a logical approach as it is really equivalent to the original fish minus a major part of the original oil. Numerous other feedstuffs, such as soybean meal, alfalfa meal, or wheat middlings are also used to produce a free-flowing dry product consisting of one-half carrier and one-half dried condensed solubles.

PROCESS METHOD

Condensed fish solubles is one of two by-products produced by the wet reduction of whole fish to fish meal. Briefly, the production of condensed fish solubles by the "wet reduction" process involves cooking whole fish (e.g., menhaden) and subjecting the cooked fish to screw-type presses. The liquid fraction which passes through the screens of the presses is collected and separated by first passing through a vibrating screen to remove suspended material. The remaining liquor is either pumped into settling tanks for gravity separation or, more commonly, centrifuged to separate the oil and aqueous portion. Usually the centrifugation system consists of a three-phase centrifuge designed to separate oil, water, and suspended material. The aqueous portion in these centrifuges is collected in large storage tanks. During this storage process usually a quantity of sulfuric acid, or occasionally phosphoric acid, is added to the stickwater until a pH of 4.5 is reached (normal pH 6-7.0). The storage tanks are heated by steam coils to a temperature of approximately 150°F for 30 min to coagulate the proteins. The suspended and coagulated proteins are removed by centrifuges, and the free oil is removed by oil-separating centrifuges. The solid materials are dried on press cake and the liquid is called "stickwater." Table 1 shows the composition of several samples of stickwater produced in 1970. These samples contained an average of about 7% total solids and about 5% protein. The amino acid profile indicates that this protein is gelatinous in nature because of the relatively high glycine, proline, and alanine content.

Stickwater is then concentrated by means of vacuum evaporation, generally operated in units of three or more. Thus, the terms "triple effect" or "quadruple effect" are applied to the evaporation procedure. The evaporators may be horizontal or vertical, depending on the position of the steam tubes used for heat. Each evaporator consists of a series of tubes, usually vertical, holding the liquor and surrounded by steam. The tubes passing through the evaporator allow the vaporized water to escape at the top, and the partially evaporated product passes to the next unit at a lower position in the evaporator.

These evaporators are subjected to reduced pressure. The first unit is usually heated by low pressure exhaust steam from the boilers and is generally maintained at about 24 inches of mercury pressure (or under a slight vacuum). As the liquor reaches a predetermined concentration, it is drawn into the second unit. The vapors from the boiling liquor in the first unit are passed through the steam tubes of the second, and the liquor continues to boil by increasing the vacuum to about 28 inches of mercury.

In the third stage the process is either completed under a vacuum of about 30 inches of mercury or continued depending on the number of stages employed. When the liquor reaches approximately 50% solids, the process is finished and the solubles are stored. Thus, during the process the original material containing about 93% water is concentrated by a factor of at least seven. Other methods of condensing fish solubles have been and are used but not extensively enough to warrant further discussion here.

TABLE 1.—Chemical composition of Atlantic menhaden stickwater.[1]

Item	Amount	Item	Amount
	%		%
Protein (N × 6.25)	4.82	Valine	2.36
Moisture	93.43	Methionine	1.37
Ash	1.12	Isoleucine	1.59
Total fat	1.26	Leucine	3.34
Ether fat	0.83	Tyrosine	1.02
		Phenylalanine	2.12
	% nitrogen	Tryptophan	0.31
Ammonia	0.034	Taurine	3.55
		Asparctic acid	5.20
	% of protein	Serine	2.31
Lysine	4.45	Glutamic acid	8.22
Histidine	4.19	Proline	5.10
Arginine	1.89	Glycine	10.45
Threonine	2.06	Alanine	5.86

[1] Values are averages of data from three analyses.

TABLE 2.—Analytical data on condensed solubles.

Item	Menhaden solubles	Pacific sardine solubles	
	Lee (1956)	March (1962)	Lassen et al. (1951)
Dry solids, %	47.6 ±3.5	50.3	50.0
Crude protein, % (N × 6.25)	33.5 ±2.7	33.7	32.0
Ammonia, %	1.3 ±1.1	--	--
Corrected protein,[1] %	27.2 ±3.8	--	--
Fat, %	6.4 ±3.2	4.3	7.0
Total ash, %	9.2 ±2.0	9.2	12.0
Water-insoluble matter, %	4.5 ±1.6	--	--
Water-insoluble ash, %	0.28 ±0.21	--	--
pH	4.64 ±0.54	4.5	--
Specific gravity	1.19 ±0.03	1.2	--
Number of samples	32	?	?

[1] Corrected for ammonia-nitrogen 5.15.

COMPOSITION OF CONDENSED FISH SOLUBLES

Analytical data (Table 2) published by Lee (1956) showed that condensed fish solubles contained approximately 50% dry matter, which included protein (Kjeldahl nitrogen × 6.25), fat, minerals, and vitamins. According to the above author the major variable factors affecting composition were species and age of the fish, season and location of the catch, handling techniques, and type of plant equipment used during processing. Data describing other types of fish solubles produced in the United States are very scanty. However, Table 2 lists some average results for herring solubles reported by March (1962) and Lassen, Bacon, and Dunn (1951), and these appear very similar to the menhaden data.

Table 3 shows the proximate, total fat, and ammoniacal nitrogen composition of 24 condensed menhaden fish solubles samples collected during 10 months of the 1969 fishing season (Soares, Miller, and Ambrose, 1970). These samples were obtained from seven different fish meal plants located along the Middle Atlantic and Gulf coasts, and they represent regular commercial production. The methods for proximate analyses were all standard AOAC (Association of Official Analytical Chemists) methods except total fat, which is a chloroform-methanol extraction method of Bligh and Dyer that was modified by Smith, Ambrose, and Knobl (1964). Since the data from the Atlantic and Gulf samples did not differ significantly (although they are made from two different species of menhaden), it is presented together as an average. In general, these analyses indicate that the solids content is slightly more than 51%. The average concentration of protein (Kjeldahl N × 6.25) was 31.8% and that of ash was 7.8%. If these values are converted to a dry basis, they are very similar to those for menhaden fish meal reported by Kifer and Payne (1968) and Kifer, Payne, and Ambrose (1969). This is not to say that dried fish solubles is equivalent to fish meal in protein quality, but this only points out the relatively high protein content of this material even after allowing for nonprotein nitrogen (Table 3). The fat content, expressed on a dry basis is somewhat higher, however, than that found in fish meal. Ammoniacal nitrogen (which included volatile amines, etc.) makes up about 0.5% of the total nitrogen.

TABLE 3.—Proximate composition, total fat, and ammoniacal nitrogen content of menhaden fish solubles.[1]

Analyses	Average of 24 samples
	%
Protein (N × 6.25)	31.8 ±2.52
Ash	7.8 ±0.93
Ether fat	8.9 ±2.13
Total fat	11.2 ±2.09
Moisture	48.7 ±2.18
Ammonia as % N	0.5 ±0.23

[1] Soares, Miller, and Ambrose (1970).

PROTEIN

Biologically, the protein in solubles is considered inferior in quality because of its high content of gelatin, derived from fish collagen, which is low in the sulfur amino acids and almost completely devoid of tryptophan. Therefore, the essential amino acids content of the protein in condensed fish solubles is not adequate as a sole source of protein for the growth of chicks because tryptophan is deficient and the content of the other essential amino acids in condensed fish solubles is lower than that found in fish meal. Nevertheless, the protein may serve very well in a diet as a minor supplementary protein or in a diet otherwise adequate in amino acids since a 3% level of fish solubles contributes only 1% protein to the total diet.

AMINO ACIDS

Table 4 lists the amino acid composition of menhaden fish solubles published by Soares et al. (1970) and shows that solubles do contain some of the amino acids in reasonably high amount. All amino acids except available lysine, tryptophan, and cystine were analyzed by ion exchange column chromatography. Available lysine was determined by the method of Carpenter (1960). Tryptophan was determined by the method of Spies and Chambers (1948), and cystine was analyzed by a microbiological assay.

It is noteworthy that cystine averaged 1.05% of protein, which is slightly higher than the 0.9% of protein found in menhaden fish meal (Kifer and Payne, 1968). Glycine, an important amino acid in poultry rations since it is necessary for maximum growth of chicks, is the only other essential amino acid found in fish solubles at levels higher than in fish meal. As mentioned earlier, tryptophan is the first limiting amino acid based on chemical composition. Available lysine averaged about 83% of total lysine which is similar to the fish meal values that we have obtained. The taurine content is also shown, inasmuch as a recent report by Monson (1969) indicates that this amino acid may be one of the unknown growth factors. Table 4 also shows the amino acid composition of sardine and herring solubles. For the most part these data are similar to menhaden. However, some large differences exist in the histidine levels which are not explainable.

TABLE 4.—Amino acid content (% of protein) of various kinds of condensed fish solubles.

Amino acid	Menhaden solubles	Herring solubles[1]	Pacific herring solubles	Pacific sardine solubles
	Soares et al. (1970)	Laksesvela (1954)	Ewing (1963:291)	Lassen et al. (1951)
	% of protein			
Arginine	3.9 ± 0.65	5.2	4.5	4.3
Histidine	2.5 ± 0.80	0.7	6.0	5.8
Lysine	4.8 ± 0.56	4.3	4.3	4.9
Tyrosine	1.1 ± 0.20	0.7	--	--
Tryptophan	0.3 ± 0.07	0.1	0.4	0.4
Phenylalanine	2.1 ± 0.27	1.5	3.2	2.3
Methionine	1.6 ± 0.17	1.4	1.5	1.5
Cystine	1.1 ± 0.28	0.1	0.3	--
Threonine	2.1 ± 0.25	2.1	1.8	2.4
Leucine	3.7 ± 0.46	3.2	3.0	4.7
Isoleucine	1.9 ± 0.28	1.9	2.3	2.7
Valine	2.7 ± 0.35	2.5	3.4	3.0
Glutamic acid	8.1 ± 0.94	7.5	--	8.4
Glycine	8.7 ± 1.50	10.9	10.9	--
Proline	4.5 ± 0.60	--	--	6.7
Taurine	3.2 ± 0.50	?	--	--
Available lysine	4.0 ± 0.62	--	--	--
No. of samples	24	--	?	?

[1] Unknown origin.

MINERALS

The ash content of condensed solubles averages about 9% and occasionally is as high as 13% of total weight (Soares et al. 1970). The major inorganic elements (Table 5) are P, Na, and K.

TABLE 5.—Inorganic elements content of menhaden fish solubles.[1]

Inorganic elements	Average	Range	
		Low	High
	Percent	*Percent*	
K	1.57 ± 0.18	1.06	1.87
Na	1.14 ± 0.28	0.70	1.67
P	0.56 ± 0.14	0.20	0.80
Mg	0.11 ± 0.03	0.08	0.17
Ca	0.06 ± 0.02	0.03	0.11
	ppm	*ppm*	
Fe	573 ± 216.00	210.	1,000.0
Al	194.5 ± 224.00	16.0	640.0
Cu	44.3 ± 49.85	1.0	120.0
Zn	18.1 ± 7.93	4.0	31.5
Ba	5.25 ± 3.85	2.0	15.2
Mn	5.22 ± 3.37	2.0	14.2
Sr	3.73 ± 1.49	1.0	7.2
B	3.05 ± 1.64	1.0	6.4
Cr	2.86 ± 0.30	2.2	3.0
Se	2.4 ± 0.44	1.4	3.6

[1] Soares, Miller, and Ambrose (1970) and Soares and Miller (1970).

Chloride which is not included in Table 5 is also present in amounts about equal to Na. Others that are present in lower amounts include: Mg, Ca, Fe, Al, Zn, and Mn. The trace elements that are found at even lower levels include: Co, I, Ag, B, Ba, Cr, Li, Ni, Rb, Sr, Si, Se, and perhaps others not yet identified. Calcium and phosphorus analyses were determined by the method of Kingsley and Robnett (1958) as adapted for the Technicon. All other elements were determined by emission spectographic analysis.

These data show that the calcium and phosphorus levels are expectedly very low compared to fish meal since the major portion of these two elements are found in the bone which remains with the meal. Most of the other minerals in fish solubles also occur in lower concentrations than in fish meal. Selenium, however, tends to be found in concentrations that are equal to or greater than fish meal. Three minerals—aluminum, copper, and iron—were detected in quite variable concentrations. The average concentration of auminum in all solubles samples is somewhat lower than that reported by Kifer and Payne (1968) for fish meals from both the Atlantic and the Gulf coasts. The aluminum content of solubles from Atlantic coast plants was, however, considerably lower than that of menhaden fish meals, whereas the aluminum content of Gulf coast solubles was somewhat higher. Similar differences in aluminum content (unpublished data) were found in Gulf and Atlantic menhaden fish protein concentrate (FPC) made at the College Park Laboratory, starting with raw fish and using stainless steel equipment under aseptic conditions. Consequently, the higher aluminum content appears to occur in the Gulf species itself rather than as a contaminant after they are caught.

Selenium has become a focal point in trace mineral research since Schwarz and Foltz (1957) and Nesheim and Scott (1958) showed that it is essential for the prevention of dietary liver necrosis in rats and of encephalomalacia, exudative diathesis, and muscular dystrophy in chicks. Thompson and Scott (1968) have suggested that the range of 0.15 to 0.2 ppm is the desirable concentration for selenium in practical poultry diets. As little as 0.05 ppm selenium in the form of sodium selenite, however, has been found to prevent the physiological abnormalities mentioned above.

So far, the Food and Drug Administration has not permitted chemical compounds containing selenium to be added to the rations of livestock. For this reason, natural sources are currently the only available means of supplementing selenium in the diet. Fish meal has been shown to be a rich source of selenium by Kifer and Payne (1968) and Kifer et al. (1969).

A number of samples of fish solubles was obtained from commercial menhaden plants throughout the 1969 fishing season and analyzed for selenium. A total of 38 samples were analyzed—20 from fish meal plants along the Atlantic coast and 18 from plants along the Gulf coast.

Although neutron activation analysis was used to determine the selenium content of the fish meals reported in the above-mentioned papers, we found that this method did not give reliable results with fish solubles. Consequently, a wet

chemical method (Hoffman, Westerby, and Hidiroglou, 1968) was used.

Table 5 shows the average results from all analyses. The data showed that there were higher levels of selenium in the Gulf product than in the Atlantic coast product (2.59 ppm vs. 2.22 ppm) (Soares and Miller, 1970). However, the corresponding fish meals from these two areas (Kifer et al., 1969) did not contain significantly different concentrations of selenium. This observation indicated to us that selenium is present in greater concentrations in the water-soluble portion of fish rather than in the water-insoluble solids, and the higher levels of selenium found in Gulf menhaden fish solubles may reflect leaching from the relatively high selenium soils draining into the Mississippi River or other local environmental conditions. Further research, however, may reveal other explanations for these differences.

Regardless of whether or not Gulf menhaden solubles or Atlantic menhaden solubles are used in feeds, a level of 2-2.5% will supply the minimal level of 0.05 ppm selenium in the diet based on total chemical analysis.

Availability determinations of selenium in fish meal and solubles are now in progress. To date there is some indication that this selenium source is not as available as sodium selenite (Miller and Soares, 1972; Scott, pers. Comm. to Morris and Levander, 1970).

VITAMINS

The fat-soluble vitamins are present in small quantities in condensed fish solubles. In contrast, the contents of the various water-soluble vitamins are at least 50% greater in the condensed solubles than in fish meal. Fish solubles are considered very rich sources for vitamin B_{12}, choline, niacin, and one or more unknown factors.

Table 6 lists data from six reports on the vitamin content of condensed fish solubles. The data are somewhat spotty and are often labeled "condensed fish solubles" with little or no details on its origin. The data are particularly deficient in regards to the fat soluble vitamins, inositol, pyridoxine, and folic acid. However, there seems to be reasonable reliability in the values given for the remaining vitamins. In particular, each kilogram of solubles contains about 4,400 mg of choline, 270 mg of niacin, 38 mg of pantothenic acid, 11 mg of riboflavin, 0.5 μg of biotin, and 440 μg of vitamin B_{12}.

NUTRITIVE VALUE

METABOLIZABLE ENERGY AND NUTRIENT DIGESTIBILITY

Metabolizable energy (ME) is the energy derived from a feedstuff after subtracting from the gross energy value the amount of energy lost

TABLE 6.—Vitamin content of condensed fish solubles.

Vitamin	Source						Average
	1	2	3	4	5	6	
Choline, ppm	4,028.0	--	--	5,300.0	2,960.0	--	4,429.0
Niacin, ppm	169.0	307.0	325.0	230.0	308.0	--	268.0
Pantothenic acid, ppm	35.0	32.3	40.0	45.0	43.1	33.0	37.7
Folic acid, ppm	--	--	--	--	1.3	0.8	1.1
Inositol, ppm	--	--	--	--	352.0	--	352.0
Riboflavin, ppm	14.5	6.9	20.0	7.7	--	4.0	10.6
Pyriodoxine, ppm	--	8.3	--	--	--	34.0	21.2
Thiamine, ppm	5.5	2.9	4.0	--	--	5.0	4.4
Biotin, ppb	0.2	1.3	--	0.3	0.1	--	0.5
Vitamin B_{12}, ppb	--	640.0	--	400.0	550.0	180.0	443.0
Vitamin A, IU/g	--	360.5	--	--	--	5.8	183.0
Vitamin D, IU/g	--	55.0	--	--	--	--	55.0
Vitamin E, IU/g	--	--	--	6.0	--	--	6.0

[1] 1. National Research Council (1968).
2. Hideo, Murayama, and Yanase (1961).
3. Lassen, Bacon, and Dunn (1951).
4. Scott, Nesheim, and Young (1969:440).
5. Ewing (1963:291).
6. Murayama and Yanase (1960).

in the feces and urine. This parameter is universally accepted among poultry nutritionists as a valid estimate of dietary energy content and is very important in formulating least cost poultry rations.

Owing to the limited data available in the literature on the ME value of condensed fish solubles, Cuppett and Soares (in press) have conducted investigations concerning this property. Data were gathered on 10 of the menhaden solubles samples used in the analytical studies discussed earlier. The experimental design with a few modifications for convenience was similar to that used by Potter and Matterson (1960) for various common feed ingredients. In these experiments, eight 3-week-old White Rock broiler cockerels were placed in each battery pen. Each diet was fed to two groups of chicks for 5 days and excreta samples were collected for 3 days. Chromic oxide was incorporated in the diet at the 1% level as a marker. Fish solubles were fed at 0, 5, 10, and 15% levels. Analyses for proximate composition and gross energy were made on all diets and excreta samples.

The average ME value was 2.03 kcal/g which is somewhat higher than the calculated figures usually presented in feed analysis tables. These results are in good agreement with the data reported by Matterson et al. (1965) and Chu and Potter (1969) (Table 7). The ME value of all three reports averages 2.12 kcal/g (962 kcal/lb) with fat and protein digestibilities of 93.2 and 62.0%, respectively. It appears that much of the problem with lower calculated values reported in the various feedstuffs tables is due to underestimating the fat content of fish solubles.

TABLE 7.—Metabolizable energy and protein and fat digestibility evaluations of fish solubles in diets fed to young broilers and turkeys.

Source	Experimental animal	Metabolizamle energy	Fat digestibility	Nitrogen digestibility
		kcal/g	%	%
Matterson et al. (1965)	Chicken	2.094	--	--
Chu and Potter (1969)	Turkey	2.223	97.7	67.2
Cuppett and Soares (in press)	Chicken	2.030 ± 0.23	88.7 ± 2.48	56.2 ± 3.70
Average		2.12	93.2	62.0

UNIDENTIFIED GROWTH FACTOR(S)

The major contribution of condensed fish solubles is the unknown factor necessary for maximum growth of poultry and hatchability of eggs. Considerable evidence has been presented to demonstrate the existence of a stable unknown essential in condensed fish solubles. Combs, Arscott, and Jones (1954) indicated that the growth response obtained with arsanilic acid occurs only in the presence of the fish factors. The so-called fish factor is believed by Tamimine (1955) to be two components: one, organic in nature and the second, inorganic. Similar results were obtained by Steinke, Bird, and Strong (1963).

Combs et al. (1954) also reported a lack of chick growth response from fish solubles fed with penicillin. Similarly, Barnett and Bird (1956) found a lack of response with high levels of chloretetracycline. The conclusion is that the activity of the fish solubles occurs only in the presence of certain intestinal microorganisms. They also obtained no growth response when chicks were in new uncontaminated buildings. Actually, their bioassay method developed for evaluating the fish factor is dependent upon the ingestion of poultry excreta by the chicks on test. This would seem to confirm that beneficial bacteria flourish in the intestines of poultry only in the presence of the fish factor. Similar evidence exists for the essentiality of the fish factor for the hatchability of chicken and turkey eggs. However, there are some contradictory reports. The reason for the differences in the observations has not yet been elucidated.

TABLE 8.—Unidentified growth factor response from various sources of condensed fish solubles.

Reference	Animal	Fish solubles	Experimental period	Types of diet	Growth response
		%	*days of age*		*% of control*
Menge and Lillie (1960)	Chick	2	8-36	Conventional	105.0
Mason et al. (1961)	Chick	2	0-14	Conventional	122.0*
Mason et al. (1961)	Chick	2	0-28	Conventional	107.0*
Mason et al. (1961)	Chick	2	0-14	Purified	107.0
Mason et al. (1961)	Chick	4	0-28	Conventional	115.0*
Harrison and Coates (1964)	Chick	5	0-28	Conventional	113.0*
Harrison and Coates (1964)	Chick	5	0-28	All vegetables[1]	107.0*
Chu (1968)	Turkey	2-5	0-56	Conventional	106.0*
Harrison and Coates (1969)	Germ-free chick	5	0-28	Sterile conventional	104.0
Harrison and Coates (1969)	Conventional chick	5	0-28	Conventional	112.0*
Bhargava and Sunde (1969)	Chick	2	0-7	Purified	109.0*
Bhargava and Sunde (1969)	Chick	2	0-14	Purified	118.0*

[1] Only vegetable sources used.
* Statistically significant ($P<0.05$).

A compilation of recent reports (Table 8) in which the phenomena of unidentified growth factors in condensed solubles were studied brings out several interesting points. First, these data indicate that significant unidentified growth responses are still being observed even when every effort is made to supply all known nutrients in the experimental diets. Secondly, growth response seems to be maximal when the solubles content ranges from 2 to 5% of the diet and when these diets are fed to chicks for 14 to 21 days beginning with day-old birds. Growth responses tend to diminish as the birds become older. Furthermore, growth stimulations are consistently observed with battery-reared chicks fed conventional feeds or highly purified rations. Therefore, it is evident that stress, such as that found in field conditions, may not be necessary to obtain a significant growth response from feeding condensed fish solubles.

An interesting series of experiments conducted by Harrison and Coates (1964) showed that significant growth responses were obtained from chicks whose parents were maintained on conventional rations containing animal protein or all-vegetable rations. In fact, the average growth response was greater when the conventional diets were fed. In comparing the effects of feeding 5% solubles to conventional or germ-free chicks, a significant response was observed only with the conventional birds. This indicates that the presence of microbes does influence the magnitude of the growth response. However, these workers observed that the addition of a small amount of sterilized or fresh droppings to the diet caused a significant growth depression which could be counteracted by feeding fish solubles.

Miller and Soares (1972) have conducted some detailed experiments designed to study unidentified growth factors in fish solubles. They used virtually a complete chemically defined diet (Table 9) except for the sources of essential fatty acids, which were supplied as purified oils. The amino acid mixture was patterned after that of Dean and Scott (1965). The vitamins, minerals, and antioxidant were supplied in sucrose-based premixes (Miller and Soares 1972).

TABLE 9.—Basal composition for crystalline amino acid diet used to study unidentified growth factor responses in chicks.[1]

Ingredient	Amount
	g/kg
Sucrose	502.3
Crystalline amino acid[2]	225.3
Antioxidant premix[3]	2.0
Cellulose	80.0
Safflower oil	50.0
Menhaden oil	10.0
$CaCO_3$	5.0
$CaHPO_4$	26.9
Mineral mix[1]	28.5
Vitamin mix[1]	50.0
Choline Cl mix	20.0
	1,000.0

[1] Miller and Soares (1972).
[2] Dean and Scott (1965).
[3] Santoquin premixed one part with nine parts sucrose. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The diets in these experiments were balanced for energy, calcium, phosphorus, and total nitrogen. When fish solubles was added to the diets, the total nonessential amino acid content was balanced by adjusting the glutamic acid content, and the essential amino acid content was balanced by decreasing the amount of the respective crystalline amino acid in the diet. All additions of condensed fish solubles produced greater growth rates in chicks as compared to the controls.

One of the above experiments consisted of six treatments with four variables (Table 10) fed to day-old chicks (duplicate groups of 12) for 3 weeks. Diet 1 was our basic crystalline diet with no added protein whereas Diet 2 contained 5.0% fish solubles. A significant growth response was obtained by the addition of fish solubles. Diet 3 plus 0.5 ppm selenium (as sodium selenite) did not give any growth response over the control. Diet 4 containing 0.5 ppm selenium plus 0.82% proline (which Graber, Allen, and Scott (1970) suggest is an essential amino acid) gave a slight but nonsignificant response in growth. Similarly, Diet 5 with 0.5 ppm selenium, 0.82% proline, and 5% gelatin protein resulted in only a small growth response. Gelatin was incorporated in the diets because earlier experiments had shown that the presence of intact protein was beneficial to the overall growth response to crystalline amino acid diets. However, when gelatin and fish solubles (Diet 6) were incorporated in the diet, there again was a significant growth response that was similar to the response obtained with only fish solubles.

TABLE 10.—Growth response and efficiency of feed conversion of chicks fed purified diets supplemented with selenium, proline, gelatin, and fish solubles.[1]

Item	Diet					
	1	2	3	4	5	6
Se, ppm	0	0	0.5	0.5	0.5	0.5
Proline, %	0	0	0	0.82	0.82	0.82
Gelatin, %	0	0	0	0	5.0	5.0
Menhaden fish solubles, %	0	5.0	0	0	0	5.0
Weight gain[2]	[3]233	[4]279	[3]236	[3]247	[3]242	[4]286
Feed efficiency	0.62	0.58	0.64	0.64	0.67	0.54

[1] Miller and Soares (1972).
[2] Average weight (g) of 18 day-old chicks.
[3], [4] Means bearing different superscripts are statistically different ($P<0.01$).

In a further experiment by Miller and Soares (1972) Diets 5 and 6 as listed in Table 10 were irradiated with 4.5 Mrad of gamma radiation by the method described by Soares et al. (1971) and were fed to conventional and gnotobiotic White Rock chicks. The results (Table 11) of an initial experiment indicate that condensed fish solubles is capable of exerting a growth response whether or not bacteria are present. It should be noted that both groups of chicks were housed under conditions making it possible for the ingestion of excreta which most likely occurred because of the type feeders used. Therefore, these data may not be in conflict with those of Harrison and Coates (1969) who observed that germ-free chicks consuming sterile diets intentionally contaminated with sterile fecal matter exhibited growth responses when fish solubles was included in the diet whereas similar chicks fed diets with no fecal contamination showed no response to fish solubles.

SUMMARY

This review shows that condensed fish solubles (particularly those made from menhaden) is quite rich in many essential nutrients needed for livestock production. This is especially true if the composition is expressed on a dry-matter basis, since half of the product consists of water. Most essential minerals and water-soluble vitamins are found in solubles in relatively high concentrations when compared with other common feedstuffs. Fish solubles is highly digestible and rich in energy (measured as metabolizable energy) and, if expressed on a dry-matter basis

TABLE 11.—Growth response of chicks for purified diets containing selenium, proline, gelatin, and fish solubles.[1]

Environment	Menhaden solubles	Weight gain	Chicks
	%	g	*Number*
Diet 5			
Conventional	0	[2]69.6	16
Gnotobiotic	0	[2]69.5	6
Diet 6			
Conventional	5.0	[3]98.5	17
Gnotobiotic	5.0	[3]107.9	7

[1] Miller and Soares (1972).
[2], [3] Means bearing different superscripts are statistically different ($P<0.01$).

have a higher caloric density than fish meal. Currently the most important nutrient in condensed fish solubles is the unidentified growth factor because significant growth responses can be demonstrated with poultry and other species of livestock under field conditions as well as in the laboratory.

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HELMINTHS OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) FROM THE KVICHAK RIVER SYSTEM, BRISTOL BAY, ALASKA[1]

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ABSTRACT

A study of helminths infecting juvenile and adult sockeye salmon (*Oncorhynchus nerka*) leaving and entering the Kvichak River system, Bristol Bay, Alaska, was conducted in 1969. Ten helminths acquired in fresh water were found in smolts: *Diplostomulum* sp.; an unidentified trematode; *Diphyllobothrium* spp.; *Triaenophorus crassus* Forel, 1868; *Proteocephalus* sp.; *Eubothrium salvelini* (Schrank, 1790); *Neoechinorhynchus rutili* (Mueller, 1789); *Philonema oncorhynchi* Kuitunen-Ekbaum, 1933; *Rhabdochona* sp.; and *Contracaecum* sp. In addition to surviving larval stages of freshwater parasites, adults were infected by nine helminths acquired in the sea: *Gyrodactyloides strelkowi* Bykhovskaya and Polyanskaya, 1953; *Lecithaster gibbosus* (Rud., 1802); *Brachyphallus crenatus* (Rud., 1802); *Tubulovesicula lindbergi* (Layman, 1930); *Phyllobothrium caudatum* (Zschokke and Heitz, 1914); *Echinorhynchus gadi* Mueller, 1776; *Bolbosoma caenoforme* Heitz, 1920; *Anisakis* sp.; and *Contracaecum* sp. Infection incidences and intensities are tabulated where accurate data are available. Information on life histories is assembled from scattered sources, and some ecological aspects of helminths infecting Kvichak sockeye salmon are briefly discussed.

The Kvichak River system is the largest producer of sockeye salmon, *Oncorhynchus nerka* (Walbaum), among five river systems in Bristol Bay, western Alaska. Its drainage basin covers nearly 8,000 square miles and includes two large lakes, Iliamna Lake (90 miles long and up to 26 miles wide) and Lake Clark (50 miles long and up to 4 miles wide). Intensive studies on sockeye salmon from this system and the other four systems, the Wood River, Naknek River, Egegik River, and Ugashik River, have been underway since 1946 (Thompson, 1962). Recent research has been directed toward determining the biological basis for annual fluctuations in the number of seaward migrants and subsequent return of adults 2 and 3 years later, and providing a reliable estimate of the optimum escapement for each of these river systems (Burgner et al., 1969).

The survival rate for Kvichak River sockeye salmon is generally higher in the peak year of the abundance cycle than in other years since the total production from each year class comes in installments 4, 5, or 6 years later, depending on the total age of the adults when they return to spawn. The occurrence of mortality inversely related to density has been ascertained from observations, but its causes remain unidentified. Since the available records show that, generally, smolt production has been proportionate to adult escapement, it appears that losses occur primarily after the smolts leave the nursery areas, but the possibility remains that the predisposing conditions are found in fresh water. The adjustments that smolts make to environmental changes, their physiological condition, and their resistance to stress have been studied by those who seek the factors that underlie variations in survival rate among year classes in

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the sea. Parasitic infections are considered a possible factor; albeit their effects may be largely sublethal, nevertheless they might contribute to disproportionate survival rates.

A field study of the helminth fauna of sockeye salmon in the Kvichak system was commenced in 1968 and expanded in 1969. The immediate tasks were to (1) identify the parasites acquired in fresh water and those acquired in the sea, (2) determine the incidence and intensity of infections, and (3) review the available literature for information on life cycles. Earlier studies by Margolis (1963) concentrated on parasites of sockeye salmon in the North Pacific Ocean as biological indicators of continental origin; he noted that over 50 parasitic species of freshwater and marine origin are known to infect sockeye salmon occurring in the North Pacific Ocean and adjacent seas. Many of these parasites occur in other species of salmon that come from Eurasia and North America to feed and mature in these waters (Akhmerov, 1963; Mamaev, et al., 1959; Mamaev and Oshmarin, 1963; Zhukov, 1960).

MATERIALS AND METHODS

The Kvichak River system consists of Iliamna Lake and Lake Clark, their tributaries, and the Kvichak River, which leads to the sea (Figure 1). Smolts migrate seaward for a few weeks following ice breakup in late May, whereas adults return to spawning grounds in July. Samples were taken from four groups of fish in 1969 (Figure 1): 1) smolts, captured by fyke net at Igiugig, on the Kvichak River (Site I), between May 28 and June 6; 2) adults in Bristol Bay, collected by set nets at Pederson Point (Site II) during May; 3) adults in fresh water, taken by beach seine in the Newhalen River (Site III) during mid-July; and 4) spawners, collected by beach seine on spawning grounds at Finger Beach (Site IV), Woody Island (Site V), and Porcupine Island (Site VI) during August. No attempt was made to discriminate between smolts originating from Iliamna Lake and Lake Clark. Adults collected at Pederson Point in Bristol Bay were known from past tagging experiments to consist almost entirely of Kvichak sockeye.

The skin, gills, eyes, gastrointestinal tract, viscera, body cavity, and swim bladder of the fish were examined for helminths. Blood smears were prepared from each fish, gall bladder smears were made from adults, and brain tissue imprints were taken from smolts. Examinations were usually conducted on the day of capture. Thus, most helminths were recovered, tentatively identified, and counted while alive and before preservation in hot Formalin[5]-Acetic acid-Alcohol solution (standard solution). In some cases tissues were preserved in hot Bouin's solution (standard solution) for future dissection and examination for parasites. Representative specimens of cestodes and trematodes were stained in Delafield's hematoxylin and mounted for further study; nematodes were either stained

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

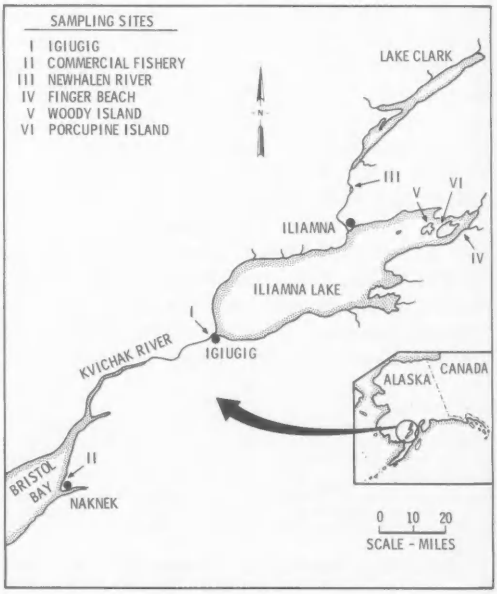

FIGURE 1.—Map of the Kvichak River system, showing sampling sites, with inset map showing its location in southwestern Alaska.

with methyl blue-lactic acid or cleared unstained in lactic acid, and examined unmounted. Blood and tissue smears were air dried, fixed in absolute methyl alcohol, and treated with Wright's blood stain.

In this report incidence and intensity are used to describe the percentage of infected hosts and the average number of parasites per infected fish, respectively. Incidences and intensities were determined with confidence for the relatively small smolts, but only the incidences were judged to be reliable for the adult fish because of difficulty in obtaining accurate counts of frequently abundant helminths.

To accurately determine the age of the host, scales from smolts and otoliths from adults were preserved and read for age, and the readings were checked against the recorded length of the fish. The smolts were from the 1966 and 1967 brood years and were designated as age 2 and age 1 according to the number of winters spent in fresh water. The adults were from the 1963, 1964, and 1965 brood years and had spent either two or three winters in the sea.

RESULTS AND DISCUSSION

Parasitological examinations were completed on 212 smolts, 88 adults from Bristol Bay, and 71 adults from fresh water. The identities and incidences of helminths in these fish are shown in Table 1 under appropriate area and age designations. No haematozoa, myxosporidians, microsporidians, leeches, or copepods were

TABLE 1.—Incidence of helminths in young and adult sockeye salmon from the Kvichak River system in 1969. (Incidence in parentheses as a percentage.)

Parasite[1]	Smolts[2]		Adults[2]						
	Kvichak River		Bristol Bay			Newhalen River		Spawning grounds	
	1.	2.	1.2	2.2	1.3 + 2.3	1.2	2.2	1.2	2.2 + 1.3
Number of fish sampled	60	152	32	46	10	33	2	26	10
Monogenea									
Gyrodactyloides strelkowi Bykhovskaya and Polyanskaya, 1953	0	0	1(3)	4(9)	1(10)	0	0	0	0
Digenea									
**Diplostomulum* sp. (spp?)	36(60)	102(67)	5(16)	7(15)	0	10(30)	2(100)	13(50)	2(20)
Lecithaster gibbosus (Rud., 1802)	0	0	29(91)	46(100)	10(100)	31(94)	1(50)	23(88)	7(70)
Brachyphallus crenatus (Rud, 1802)	0	0	3(9)	3(7)	0	3(10)	0	4(15)	1(10)
Tubulovesicula lindbergi (Layman, 1930)	0	0	0	0	0	2(6)	0	1(4)	0
Unidentified Digenea	0	2(1)	0	0	0	0	0	0	0
Cestoda									
**Diphyllobothrium* spp.	21(35)	100(66)	3(9)	6(13)	1(10)	0	0	0	0
**Triaenophorus crassus* Forel, 1868	0	4(3)	0	0	0	0	0	0	0
***Proteocephalus* sp. (spp?)	37(62)	72(47)	0	0	0	0	0	0	0
Eubothrium salvelini (Schrank, 1790)	1(2)	2(1)	0	0	0	0	0	0	0
***Phyllobothrium caudatum* (Zschokke and Heitz, 1914)	0	0	32(100)	46(100)	10(100)	33(100)	2(100)	26(100)	10(100)
Acanthocephala									
Neoechinorhynchus rutili (Mueller, 1780)	1(2)	20(13)	0	0	0	0	0	0	0
Echinorhynchus gadi (Mueller, 1776)	0	0	0	4(9)	2(20)	1(3)	0	0	0
***Bolbosoma caenoforme* Heitz, 1920	0	0	22(69)	34(74)	6(60)	4(12)	0	7(27)	1(10)
Nematoda[3]									
Philonema oncorhynchi Kuitunen-Ekbaum, 1933[4, 5]	60(100)	140(92)	23(72)	38(83)	7(70)	32(97)	2(100)	26(100)	9(90)
Rhabdochona sp.	0	8(5)	0	0	0	0	0	0	0
Anisakis sp. (spp.?)[5]	0	0	--	--	--	--	--	--	--
Contracaecum sp. (spp.?)[5]	1(2)	18(12)	--	--	--	--	--	--	--
*Other nematodes[6]	--	--	31(97)	45(98)	10(100)	33(100)	2(100)	20(77)	9(90)

[1] * = larvae (in fish intermediate host), ** = postlarvae (sexually undeveloped parasite).
[2] Age designation is based on Arabic numerals corresponding to the number of winters lived. Freshwater age precedes the dot, salt water age follows the dot; i.e., 2.2 = adult, 2 winters in fresh water, 2 winters in the sea.
[3] Examination of adult sockeye for nematodes was restricted to the digestive tract, viscera and body cavity.
[4] Incidence of *P. oncorhynchi* in smolts was based on larvae in the swim bladder; in adults, on encystation of mature worms among the viscera and on body cavity wall.
[5] Of nematodes preserved from Bristol Bay adult sockeye, the ratio (in total numbers) of *P. oncorhynchi* to *Anisakis* to *Contracaecum* was about 1:2:1.5.
[6] Primarily *Anisakis* and *Contracaecum* in Bristol Bay adult sockeye, primarily *Anisakis* in adults reaching fresh water.

detected. Some of the genera of helminths may be represented, in fact, by more than one species since specific identification of some immature forms was not possible. The parasites are considered under five taxonomic groups: Monogenea, Digenea, Cestoda, Acanthocephala, and Nematoda. Some data on the life cycle of each parasite, which are essential to an understanding of the cause-and-effect relationships for parasitic infections, are given where available.

MONOGENEA

No monogenetic trematodes of freshwater origin were found on the gills of smolts, although *Tetraonchus alaskensis* Price, 1937 has been reported from young sockeye salmon in the Wood River system (Margolis, 1963, tables). *Gyrodactyloides strelkowi* (Gyrodactylidae) parasitized the gills of five adults taken at Pederson Point. This viviparid is specifically a salmon parasite (Margolis, 1965) and is phylogenetically related to the genus *Gyrodactylus* which parasitizes primarily freshwater teleosts. Since *G. strelkowi* lives externally on its host and is adapted only to marine conditions, it is lost soon after the return of adult sockeye salmon to fresh water.

DIGENEA

Two species of dignetic trematodes were acquired by smolts in fresh water, and three species by maturing fish in the sea.

Metacercariae of the trematode genus *Diplostomulum* (Diplostomatidae) occurred in the eye lenses of over half of the smolts. The incidence of infection was slightly less in age 1 (60%) than in age 2 smolts (67%). Infection normally occurs via furcocercous cercariae that emerge from freshwater gastropods, penetrate the skin of various fish, and localize in their eyes as metacercariae. Studies on *Diplostomum spathaceum* (Rud., 1819), a widely distributed Palearctic species that matures in the intestine of gulls, indicate that infection of fish does not occur in brackish water, a result of the absence of required freshwater molluscan hosts (Cichowlas, 1961). The incidence of *Diplostomulum* in returning adults taken at Pederson Point was significantly lower (15-16%) than in departing smolts, but still less than in adults penetrating into the headwaters of the Kvichak; thus those fish that returned to spawn were again exposed to cercariae after re-entry.

Variable numbers of three hemiurid trematodes were found in the stomach and upper intestine of adult sockeye salmon from Bristol Bay: *Lecithaster gibbosus*, *Branchyphallus crenatus*, and *Tubulovesicula lindbergi* (Hemiuridae). All were acquired in the marine environs by ingestion of crustacean plankters that serve as second intermediate hosts and carry the stages maturing in sockeye salmon. The incidence of *L. gibbosus* in sockeye salmon at Pederson Point exceeded 90% and was only slightly less in adults collected from the spawning grounds. Margolis (1963) noted that the rate of infection by *L. gibbosus* in sockeye salmon was lower in offshore than in inshore areas and deduced that most parasites in maturing fish were acquired after they re-entered coastal waters. This conclusion was supported by data of Mamaev and Oshmarin (1963) for sockeye salmon taken along the Soviet eastern coast and of Boyce (1969) for those from British Columbia waters. The acquisition of the parasites in coastal areas is presumably related to the relatively high abundance of molluscan first intermediate hosts. Boyce (1969) found that marine snails of the genus *Thais* were the first intermediate host and the marine copepods *Centropages abdominalis* and *Pseudocalanus minutus* were the second intermediate hosts of *L. gibbosus* in coastal areas of British Columbia. *L. gibbosus* matures in 1 to 2 weeks and has a lifespan of about 2 to 9 months in pink salmon, whereas *Tubulovesicula lindbergi* matures in 2 to 4 months and lives at least 31 months in chum salmon (Margolis and Boyce, 1969). Thus most trematodes acquired in coastal waters and maintained in the digestive tract of sockeye salmon during their migration into the Kvichak system are likely to persist until their postspawning death.

Branchyphallus and *Tubulovesicula* were of comparatively low incidence, and *Hemiurus levinseni* Odhner, 1905, a marine hemiurid known to infect adult salmon in the North Pacific, was

not found. The distribution of these parasites appears to be somewhat sporadic. Data tabulated by Margolis (1963) from Bristol Bay sockeye salmon in 1957 suggest that *B. crenatus* is more common (40% incidence) in Kvichak fish than our samples indicate, but concur on the relative scarcity of *T. lindbergi* and absence of *H. levinseni*.

CESTODA

The tapeworms belonged to five genera and, with the exception of *Eubothrium*, were either plerocercoid larvae, encysted among the viscera, or sexually immature, postlarval forms in the intestinal lumen. Presumably all infections were acquired by ingestion of cyclopid and/or diaptomid copepods containing infective procercoids.

Encysted plerocercoids belonging to the genus *Diphyllobothrium* (Diphyllobothriidae) were fairly common in the stomach walls of many smolts but also occurred, though less frequently, in the liver, spleen, and the intestinal wall. Since the incidence of infection was higher in smolts of age 2 (66%) than in those of age 1 (35%), it appears that the plerocercoids accumulate with continued sojourn of the fish in the lake environment. The incidence of *Diphyllobothrium* larvae in the viscera of adult sockeye salmon from Pederson Point, which had spent 2 or 3 years in the sea, was significantly lower (9-13%). Diphyllobothriasis is common in freshwater salmonids of the Northern Hemisphere (Becker and Brunson, 1967), but the identities and life cycles of many forms remain unclear. Vik (1964) reviewed the bionomics of *Diphyllobothrium*, and Stunkard (1965) and Meyer (1966) discussed taxonomic problems. Rausch (1954) described the plerocercoids of *D. ursi* Rausch, 1954, from juvenile and adult sockeye salmon and the adult cestodes from bears on Kodiak Island, Alaska. Rausch and Hilliard (1970) identified six species of *Diphyllobothrium* indigenous in Alaska and noted that several occur as plerocercoids in salmonids and other freshwater fishes. In all probability, the plerocercoids present in Kvichak sockeye salmon represent two or more species with different definitive hosts (birds or mammals) but with otherwise similar life cycles.

Larvae of *Triaenophorus crassus* (Triaenophoridae) were encysted in either the body cavity or muscle of only four smolts, all of which were age 2. None was detected in returning adults, although apparently the plerocercoids can survive in ocean-dwelling salmon for 4 or 5 years (Margolis, 1963). This cestode is specific for its definitive host, the northern pike (*Esox lucius*); however, the first intermediate host may be one of several species of freshwater copepods (Watson and Lawler, 1965), and the second is a planktivorous fish. Reviews of *T. crassus* and other species of *Triaenophorus* were made by Miller (1952), Lawler and Scott (1954), and Michajlow (1962). In the Kvichak system, the incidence of *T. crassus* in sockeye salmon smolts is apparently low, but it varies among other river systems bordering Bristol Bay (Margolis, 1963, 1967). The fact that Kvichak smolts are largely pelagic apparently accounts, in part, for the low incidence of infection by *T. crassus*, since copepods infected with procercoids will occur most abundantly in shallow, marshy inshore areas inhabited by pike. (Field observations by the second author in 1958 indicated that the incidence of *T. crassus* plerocercoids was higher in smolts from Lake Clark, which has a comparatively greater proportion of shoreline to water mass, than in those from Iliamna Lake.)

Tiny postlarvae of *Proteocephalus* sp. (Proteocephalidae) occurred in the intestinal lumen of about half of the Kvichak smolts, but the incidence of infection was lower in age 2 fish (47%) than in age 1 (62%). Presumably these cestodes had recently emerged after infected copepods were ingested and the smolts were fortuitous hosts in which further development was restricted. The larvae of *Proteocephalus* in age 2 smolts were no further advanced than those in age 1, and the incidence of infection was lower (47 versus 62%); thus it appears that these cestodes soon perish. No *Proteocephalus* occurred in returning adult sockeye. The favored definitive hosts of this parasite probably are resident fish in the Kvichak system.

Eubothrium sp. (Amphicotylidae), probably *E. salvelini* Schrank, 1790) on ecological

grounds, occurred as adults in the intestines of three smolts. This holarctic cestode appears to be rare in sockeye salmon in major Bristol Bay watersheds (Margolis, 1963, tables) but is sometimes common in salmonids from other areas. Infections of about 35% incidence occurred in sockeye smolts leaving Babine Lake, British Columbia, in 1952 and 1953 (Dombroski, 1955), and an incidence of 20-30% among these migrants has been recorded recently (Smith and Margolis, 1970). There is no teleost intermediate host for *Eubothrium*, and juvenile sockeye salmon become infected directly by ingestion of planktonic copepods carrying procercoids, such as *Cyclops strenuus* in Norway (Vik, 1963). *E. salvelini* apparently does not survive the sojourn of growing sockeye salmon at sea. Recent evidence suggests that cestodes of a related species, *Eubothrium crassum* (Bloch, 1779), found in returning Atlantic and Pacific salmon in rivers, are rarely the same worms carried to sea by smolts but are of marine origin, and that two biological races, one marine and one fresh water, exist (Kennedy, 1969).

Postlarval forms of *Phyllobothrium caudatum* (Tetraphyllidea) were found in the digestive tract of all fish taken at Pederson Point, the Newhalen River, and the spawning grounds (mean intensity, 16/fish). Little decrease was apparent in either incidence or intensity of infection in adults that reached fresh water despite their cessation of feeding. The unencysted postlarvae exist in a state of arrested development. They live in captive juvenile pink and chum salmon in seawater for at least 8 months with no change in form, but grow from 1 to 4 or 5 mm (Boyce, 1969). Moderate to heavy infections of phyllobothriids are acquired by nearly all species of salmon feeding in the North Pacific (Akhmerov, 1963; Margolis, 1963; Zhukov, 1960) and their numbers are apparently cumulative. The mature form and the definitive host of this cestode remain unknown, and some taxonomic confusion exists as to its specific identity. Williams (1968), who reviewed the Phyllobothriidae, concurred with Margolis (1963) in identifying the postlarvae from sockeye salmon in the North Pacific and adjacent seas as *P. caudatum*. The hosts of larval *Phyllobothrium* include marine cephalopods, elasmobranchs, teleosts, and mammals, but the mode of infection and subsequent behavior of the late procercoid and developing plerocercoid are not known (Williams, 1968).

ACANTHOCEPHALA

The incidence of *Neoechinorhynchus rutili* (Neoechinorhynchidae) among the smolts was low and tended to be greater among those of age 2 (13%) than those of age 1 (2%). None was found in returning adult sockeye. Tabulated data by Margolis (1963) indicate that this acanthocephalan does not survive the sockeye's ocean residence. *N. rutili* developed rapidly, and hence the parasites carried in the intestine of smolts were sexually mature. Margolis (1963) listed an incidence of 8% in Kvichak smolts examined in 1956.

N. rutili is an euryxenous parasite with wide dispersal in freshwater habitats of Eurasia and North America (Van Cleave and Lynch, 1950) and is the only species of the genus found in European freshwater fishes (Bullock, 1970). The only known intermediate host of *N. rutili* in North America is the ostracod *Cypria turneri* (Merritt and Pratt, 1964), whereas in Great Britain there are two known intermediate hosts, the ostracods *Cypria ophthalmica* and *Candona candida* (Walker, 1967). The ostracod *Cyclocypris laevis* and two species of *Sialis* (Insecta) are known to transmit the infective larvae to fish in Europe (Ginetsinskaya, 1958).

Echinorhynchus gadi (Echinorhynchidae) occurred in six adult sockeye salmon from Pederson Point. According to Margolis (1965), this acanthocephalan is widely distributed in northern seas; it is common in sockeye salmon taken off the Kamchatka Peninsula of the USSR but is generally rare in salmon captured in other areas, including the North American coast. *E. gadi*, like *N. rutili*, is an euryxenous parasite but differs in that it originates in the sea. It occurs in many families and genera of teleosts in the North Pacific and North Atlantic, particularly demersal fishes, but most commonly in the cods (Gadidae) (Linton, 1933; Margolis, 1965; Sindermann, 1966). The first intermediate hosts are marine amphipods, such as *Gammarus lo-*

custa, Amphithoe rubricata, and *Pontoporeia femorata* in European waters (Ginetsinskaya, 1958) and *Cyphocaris challengeri* off the coast of British Columbia (Ekbaum, 1938). Infections are gradually lost because of the relatively short lifespan of the mature parasite when anadromous salmon cease feeding (Ginetsinskaya, 1958).

Postlarval forms of *Bolbosoma* sp. (Polymorphidae), probably *B. caenoforme* on ecological grounds, were common in the intestine of adult sockeye salmon from Pederson Point (60-74% incidence), but the incidence decreased over a 3-month period as the fish penetrated into fresh water. The decrease in incidence was accompanied by a decrease in mean intensity from about 5 (range, 1-15) in fish taken from Bristol Bay to about 2 (1-6) in fish collected on the spawning grounds. Maturation of *B. caenoforme* appears to be inhibited in salmon, which are presumably accidental hosts. The definitive hosts are believed to be marine mammals. Nevertheless, there is a wide distribution and high incidence of this acanthocephalan in salmon feeding in waters of the North Pacific (Akhmerov, 1963; Mamaev et al., 1959; Margolis, 1963, table).

Four species of juvenile *Corynosoma* (Polymorphidae) were reported in sockeye salmon from the North Pacific and adjacent seas by Margolis (1958), but the incidence was less than 2%. One species, *C. villosum* Van Cleave, 1953, was reported in Ugashik River sockeye salmon in 1957 but not in other Bristol Bay adults (Margolis, 1963, table). No *Corynosoma* were found in Kvichak adult sockeye salmon during this study.

NEMATODA

Philonema oncorhynchi (Philometridae) was the common nematode parasitizing the smolts, but the incidence from our data was higher in age 1 (100%) than in age 2 (92%). Larval forms commonly occurred in the swim bladder, occasionally in the kidney, and rarely in other visceral organs. The larvae apparently leave the swim bladder or tissues during the sockeye salmon's sojourn at sea and enter the body cavity, where they mature in synchrony with maturation of the host (Margolis, 1970). In the adults taken at Pederson Point, the incidence of *P. oncorhynchi* exceeded 70%, and the mature worms were localized in the body cavity. Data tabulated by Margolis (1963) indicate that the incidence of this nematode in sockeye salmon returning to major Bristol Bay tributaries is generally high (92 - 100%) and that the intensity of the infections is relatively high (averaging 11-61 parasites/fish). There is little doubt that the very small nematodes reported in sockeye salmon smolts leaving Bristol Bay tributaries in 1956 (100% incidence) by Margolis (1963) were, as he assumed, larvae of *P. oncorhynchi.*

Recent data have elucidated the life cycle of this dracunculoid nematode, which infects salmonids in fresh water on both borders of the North Pacific Ocean. Gravid worms are presumably discharged along with eggs when the adult fish spawn, the worms burst to liberate thousands of larvae, and the larvae are ingested by a suitable copepod intermediate host, such as *Cyclops bicuspidatus* (Platzer and Adams, 1967). Invasive larvae are liberated from infected copepods in the stomach of sockeye smolts, penetrate the gut wall, and move through either the coelomic cavity or the mesentery and associated tissues to the swim bladder within 18 hr (Adams, 1969). Numbers of larvae carried by smolts moving seaward may reach the hundreds (Margolis, 1970), since the intensity of infection tends to increase during the freshwater life of the planktivorous smolts.

Two other nematodes were acquired by the smolts, *Rhabdochona* sp. and *Contracaecum* sp. *Rhabdochona* (Rhabdochonidae) occurred in the intestine of a few age 2 smolts (5%) but not in adult sockeye salmon taken at Pederson Point. Although little is known of the bionomics of various species of *Rhabdochona,* these nematodes are common in various North American freshwater fishes (Choquette, 1951). The incidence of *Contracaecum* was also low in age 1 (2%) and age 2 (12%) smolts, and about one immature nematode was found encysted in the viscera of each infected fish.

Contracaecum and *Anisakis* (Heterocheilidae) are cosmopolitan parasites of many marine fish-

es. Anadromous salmonids carry the parasites into fresh water. Nearly all adult sockeye salmon taken at Pederson Point harbored quantities of larval anisakids belonging to these two related genera. Accurate records of adults infected with either *Contracaecum* and/or *Anisakis* were not obtained, but the actual combined incidence was probably 100%, as tabulated for Bristol Bay sockeye salmon returning in 1957 by Margolis (1963). In our study, these helminths were listed simply as nematodes because of the difficulty of individually examining large numbers of parasites scattered throughout the viscera of the large fish. On the basis of preserved material from adult sockeye salmon taken at Pederson Point, the ratio of *P. oncorhynchi* to *Anisakis* to *Contracaecum* was about 1:2:1.5 by total numbers.

According to Margolis (1970), the typical life cycle of nematodes belonging to the superfamily Ascaridoidea (including all anisakids) occurring in fishes probably involves three hosts—a crustacean or other invertebrate as first intermediate host, a fish as second intermediate host, and a piscivorous fish, bird, or mammal as the definitive host—depending on the genus or species concerned. Whether the larval *Contracaecum* found in Kvichak smolts in this study are identical with those in returning adult sockeye salmon is problematical, but it is possible that stages liberated from spawning fish were acquired by some smolts.

INTENSITIES OF FRESHWATER HELMINTHS IN SMOLTS

Ten helminths with life cycles involving initial transfers in the freshwater environs were harbored by migrating Kvichak smolts (Table 1). One of the objectives of this study was a determination of the potential effects of these helminths, however subtle and indirect they may be. Some indication is provided by the intensity of infections in correlation with the site selected for latent or active development.

Ecologically speaking, the intensity of infection is roughly correlated with the incidence of infection because the more abundant the parasite, the greater will be the distribution of infections among all available hosts. Moreover, the higher the incidence and/or intensity of infection, the more favorable will be the sum of all synecological factors involved in sustaining a particular host-parasite association.

The intensities of the five common helminths acquired by smolts in Iliamna Lake and Lake Clark are given in Table 2. Accurate counts were not made of the ubiquitous *Philonema oncorhynchi* and data on the adventitious *Proteocephalus* sp. are omitted. Some additional data are included from smolts captured in previous years, preserved in Formalin, and subsequently examined. Of these helminths four occurred as immature or larval forms in the body cavity, tissues, or organs.

The acanthocephalan *Neoechinorhynchus rutili* inhabits only the intestine of smolts, where it rapidly matures. In this favored location the female releases the eggs, these are passed externally, and the worms eventually degenerate. Infection burdens were found to be low in this study, with usually one but sometimes two parasites per host. With such low intensities, fertilization of eggs in the intestine (which requires association of a male and a female) is exceptional and the parasite tends to be self-limiting. Consequently, the principal definitive hosts in the Kvichak system are probably resident fishes that sustain an infection foci. The data, though scanty, suggest that infection of smolts occurs primarily in Iliamna Lake since samples from Lake Clark and its tributary, the Newhalem River, harbored none. Data presented by Margolis (1963) for 25 Kvichak smolts in 1956 list an incidence of 8% and a mean intensity of one parasite per fish.

Diplostomulum sp., *Diphyllobothrium* spp., and *Triaenophorus crassus* persist in sockeye salmon as larvae throughout the life of their host. Completion of their life cycles requires that an infected fish be eaten by a predator or scavenger in which the parasite is able to mature and shed its eggs. *Philonema oncorhynchi* transforms from larvae to adult in sockeye and is liberated during the spawning act or upon the host's death.

Both the incidence and intensity of *Triaenophorus crassus* were low in Kvichak smolts in this

TABLE 2.—Incidence and intensity of some helminths from juvenile sockeye salmon in the Kvichak River system in 1961, 1966, 1968, and 1969. (Incidence is the percentage of the sample infected; mean intensity, from infected fish only, in parentheses.)

Parasite[1], [2]	Kvichak River			Iliamna Lake	Newhalen River	Lake Clark
	1966	1969		1968	1961	1968
	1.	1.	2.	2.	1.	2.
Number of fish sampled	50	60	152	50	50	50
**Diplostomulum* sp. (spp.?)	--	60(2.0)	67(2.5)	--	--	--
**Diphyllobothrium* spp.	24(1.3)	35(1.2)	66(1.8)	28(1.1)	26(2.0)	2(1.0)
**Triaenophorus crassus*	0	0	3(1.3)	0	20(1.5)	0
Neoechinorhynchus rutili	10(1.2)	2(1.0)	13(1.3)	2(1.0)	0	0
**Philonema oncorhynchi*	100	100	92	100	100	91

[1] * = larval parasites (in fish intermediate host).
[2] Examinations other than in 1969 were taken from fish preserved in 10% Formalin, which restricted accurate counts of *Diplostomulum* and *P. oncorhynchi*.

study (Table 2). Data from Kvichak smolts in 1964 and 1965 (Margolis, 1967) suggest that the incidence of *T. crassus* in Kvichak smolts is generally low, less than 3%, and that the usual intensity is but one or sometimes two plerocercoids per parasitized fish. *T. crassus* has been found regularly in samples from the Wood and Naknek Rivers but only occasionally in those from the Ugashik and Kvichak Rivers (Margolis, 1967).

Metacercariae of *Diplostomulum* occurred in the eye lenses of 60% of the Kvichak smolts in this study but the mean intensities were low, 2.0 to 2.5 parasites per fish. An incidence of 48% (25 fish examined) and an intensity of 2.0 in Kvichak smolts studied in 1956 were tabulated by Margolis (1963).

Margolis (1963) found that 15% of the Kvichak adults returning in 1957 were infected with *Diplostomulum* (mean intensity, 2) and our data (Table 1) closely agree. Thus the incidence but not the intensity of the infections is significantly lower in returning adults than in smolts. Whether this is due to the loss of metacercariae in the lenses of many ocean-dwelling fish, as suggested by Margolis and by Dogiel (1966), or perhaps to disproportionate loss of infected fish as our data hint is conjectural.

The incidence of *Diphyllobothrium* in age 2 Kvichak smolts was 66% from data obtained during this study, but intensities were usually low, with one or two plerocercoids per infected fish. Of the smolts examined from Bristol Bay tributaries in 1957 by Margolis (1963), Kvichak fish ranked second in level of incidence (52%), whereas those from the Egegik River were first with 88% incidence, and those from the Naknek were third with 20% incidence.

Data obtained in this study and provided by Margolis (1963) indicate that nearly all smolts leaving the major rivers of Bristol Bay are infected with larvae of *Philonema oncorhynchi*, but that the intensities vary widely, often exceeding 50 per fish.

It is beyond the scope of this paper to postulate on any effects that the parasites of Kvichak sockeye salmon may have upon the survival of their host. There is ample evidence in the literature that, given certain pre-disposing conditions, direct mortalities from mechanical damage, histopathological changes, and measurable effects upon size and growth rates of parasitized fish do occur. Any factor that results in environmental discrimination, such as the presence of internal and external parasites, would tend to lessen the chances of a fish for survival. The question of whether or not the various parasites occurring in Kvichak sockeye salmon, alone or in combination, cause losses of ecological significance remains to be explored.

POSTSCRIPT

David A. Pennell entered the College of Fisheries of the University of Washington as a graduate student in the fall of 1968. On August 1969, he was involved in a fatal airplane accident while collecting material in the field for his M.S. dissertation on the parasites of sockeye salmon in Bristol Bay, Alaska. This paper is published posthumously in honor of this promising and highly dedicated young man.

Dr. C. Dale Becker undertook to complete the manuscript from a preliminary analysis and report by Mrs. Nora R. Scofield. Supplemental data, collected earlier by Dr. Becker while with the Fisheries Research Institute, have been included in this paper. Assistance and advice were given by Drs. A. K. Sparks and O. A. Mathisen throughout the course of the study.

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AN ECOLOGICAL STUDY OF *GOBIOSOMA BOSCI* AND *G. GINSBURGI* (PISCES, GOBIIDAE) ON THE GEORGIA COAST[1]

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ABSTRACT

The ecology of two species of "scaleless" gobies, *Gobiosoma bosci* and *G. ginsburgi*, from estuarine and beach waters around Sapelo Island, Ga., is compared. Small patches of oysters, in addition to oyster reefs, are important nesting areas for both species. Numerous invertebrates and five other fishes are characteristic of the oyster patches. Habitats common to both species include reefs and patches of oysters, bottoms of estuarine rivers of moderate to high salinity, and burrows in an eroding clay deposit off Sapelo Beach. In contrast to *G. bosci*, *G. ginsburgi* ranges offshore, is thought to spawn in deep water, and is not found in fouling communities, marsh pools, and low salinities.

These gobies are sexually dimorphic in genital papilla, body size, and color. They nest in oyster shell. Males incubating and guarding their own eggs are cannibalistic on eggs of other individuals, apparently having the ability to distinguish their own nests or eggs from those of other individuals. Higher egg counts in nests than in ovaries prove that *G. bosci* is polygamous.

The spawning seasons of *G. bosci* and *G. ginsburgi* are apparently similar. The season of *G. bosci* is protracted to the south and correlates with water temperature.

Our study of the reproduction and ecology of the two species of "scaleless" gobies, the naked goby (*Gobiosoma bosci*) and seaboard goby (*G. ginsburgi*), was initiated when they were discovered incubating eggs in oyster shells at Sapelo Island, Ga. This provided the opportunity to compare certain aspects of the life history of these two secretive species and analyze their ecological relationship to oyster communities. There are some published ecological information on these two species (Dawson, 1966, 1969, and references therein) and some scattered reports on reproduction that are partially summarized by Breder and Rosen (1966).

Since most species of *Gobiosoma* are tropical (Böhlke and Robins, 1968), the genus probably originated in the tropics. However, the low spawning threshold of *G. bosci*, about 20°C (Nelson, 1928), suggests a temperate-water origin for this species. *G. bosci* ranges from Connecticut (Pearcy and Richards, 1962) and Long Island Sound to Campeche, Mexico (Dawson, 1969). *G. ginsburgi* ranges from the Wareham River and Woods Hole, Mass. (Ginsburg, 1933; Lux and Nichy, 1971), to Jekyll Island, Ga. (Dawson, 1966). *G. robustum* ranges from the Gulf of Mexico to the St. Johns River, Fla. (Tagatz, 1968), and has been found in Maryland (Schwartz, 1971). *G. longipala*, the Gulf cognate of *G. ginsburgi*, is considered a distinct species (Dawson, 1966). The similarity of these two species, however, leaves little doubt that they are derived from a common ancestor whose distribution was split by the emerged Florida plateau, which now functions as an ecological and/or physical barrier. In contrast, Atlantic and Gulf populations of *G. bosci* have not diverged recognizably.

G. bosci and *G. ginsburgi* are easily distinguished. *G. ginsburgi* has two ctenoid scales

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on each side of the caudal fin base and *G. bosci* is entirely scaleless. The best field characteristic for differentiating the two species is the color pattern on the sides of the body. In *G. bosci*, the sides are dark with eight or nine narrow, light bars that are of uniform width, and there are no dark spots along the lateral midline. During the breeding season the light bars of some males are obscured by increased pigmentation. In *G. ginsburgi*, the light bars broaden below the lateral midline, and there are dark spots or lines where the midline crosses the dark bars.

G. bosci and *G. ginsburgi* occur in large oyster reefs and small isolated patches of oysters that are partially exposed at low tide. The total area occupied by the small patches is relatively great since they border the maze of tidal creeks and occupy shallow mud flats in the lower reaches of the estuary where salinity is generally above 15‰. Two such sites were selected for detailed study. One is the mouth of Big Hole lagoon that separates Sapelo Island Beach from Cabretta Beach. The bottom is predominantly sand, but ebb tide currents have eroded deposits of hard clay that are derived from Pleistocene salt marshes. The gobies occupy the small reefs in sand and clay bottoms and often nest in isolated hinged shells that are stabilized in the clay. The second study site is a creek that runs under the boat house of the University of Georgia Marine Institute and that winds through the salt marsh. This is a typical salt marsh creek with a mud and shell bottom and mud banks that are bordered with cord grass (*Spartina alterniflora*). Small reefs along the bank and bottom are exposed when the approximately 2.1-m tide is low.

Some specimens were obtained by seining at Sapelo Island and other specimens by sampling with a bucket dredge and otter trawl in the estuary that ranges from the oligohaline Riceboro Creek to Sapelo and St. Catherines Sounds. The 30-ft (9.1 m) seine had ¼-inch (6.35-mm) mesh. The 20-ft (6 m) wide trawl had 1¼-inch (32-mm) mesh. A June collection is from Chatham County. Dip net collections were taken beneath floating docks at Halfmoon Landing and Carrs Neck Creek. Macroinvertebrates observed in reefs were collected by hand or dip net.

HABITATS

In the Sapelo Island region most collections of *G. bosci* and *G. ginsburgi* were made in patches of oyster shells or in isolated hinged shells. *G. bosci* occurs where shells are not available in Texas (Hoese, 1966) and in grassy areas in Chesapeake Bay (Hildebrand and Schroeder, 1928). Some *G. bosci* were collected in marsh pools, as they were by Kilby (1955), and some among fouling communities (including sea squirts, hydroids, barnacles, and small oysters) on pilings, and on the underside of floating docks in summer and winter, a habitat reported by Joseph and Yerger (1956).

Extensive trawling and dredging in a Georgia estuary for 3 years produced four collections of *G. bosci* at stations where water depth ranged from approximately 4.5 to 12.0 m. Two were from part of the lower estuary where shells are abundant on the bottom, and two were from the middle part of the estuary where the bottom has various amounts of sand, gravel, mud, and debris. A few were seined in sandy areas along Sapelo Beach where cover was scarce. On 4 March 1969, 9 *G. bosci* were found along with 114 *G. ginsburgi* and 7 *Hypsoblennius hentzi* in tubular burrows in an eroding clay outcrop on Sapelo Beach. Burrows such as these, apparently made by false angel wings (*Petricola pholadiformis*), may be overwintering sites for large portions of the goby populations. Gobies and other fishes become scarce on the reefs in fall and winter. Some *G. bosci* were found in mud and debris at the edge of oyster reefs at near-freezing water temperatures (Hoese).[4] At temperatures below 20°C many *G. bosci* were found in mud-bottom marsh pools, where they apparently burrow in the mud during the coldest part of the winter, as speculated by Hildebrand and Cable (1938). A mass migration of *G. bosci* to deeper waters of the sounds in the winter is unlikely, as they were trawled in shallows (generally less than 1.2 m) throughout the year (Dawson, 1966).

[4] Hoese, H. D. Studies on fishes associated with American oysters (*Crassostrea virginica*). Unpublished manuscript filed at University of Southwestern Louisiana.

We collected *G. bosci* at temperatures of 12.7° to 31.3°C. It is known to occur at temperatures of 1.5° (Hoese, see footnote 3) to 33.2°C (Gunter, 1945).

G. bosci is euryhaline and is common in low to moderate salinities. Dawson (1966) suggested that *G. bosci* apparently departs from the size-salinity relationship described by Gunter (1945) wherein the youngest individuals predominate in the low salinities. Our data generally support Gunter's observations as our three low-salinity (0-1.9‰) collections contained only 14- to 22-mm specimens. However, Dawson (1966) found most 9.5 to 11.0-mm *G. bosci* to occur at 14.8 to 24.7‰ salinities. *G. bosci* spawns in moderate to high-salinity waters and the 4- to 15-mm pelagic larvae move upriver by an unknown mechanism (Massmann, Norcross, and Joseph, 1963). Since the smallest specimens reported by Dawson (1966) apparently were recently spawned, his observation does not disprove the size-salinity hypothesis.

Habitats of *G. ginsburgi* and *G. bosci* overlap to some degree. *G. ginsburgi* was commonly found in oyster shells at Big Hole. It was rare in the marsh creek; here only a single 16-mm *G. ginsburgi* was collected, along with 44 *G. bosci*, on 12 February 1968. *G. ginsburgi* was more abundant than *G. bosci* in burrows in the eroding clay banks on the beach as noted above and in deepwater stations in the estuary. There were nine dredge and trawl collections of *G. ginsburgi* (13 specimens) in the estuary compared with four of *G. bosci* (4 specimens). In contrast to *G. bosci*, these collections of *G. ginsburgi* were all taken in shell areas. *G. ginsburgi* ranges offshore to a depth of 45 m (Dawson, 1966). Apparently it spawns in deep water, and its young do not migrate into low-salinity water. *G. ginsburgi* occurred in three dredge collections from 1.6 to 12.9 km (about 10 m depth) off the Georgia coast. *G. ginsburgi* was not found in shallow marsh pools, fouling communities, or in low salinities. We collected it at salinities of 24.9 to 34.1‰ in the estuary, and de Sylva, Kalber, and Shuster (1962) collected it at 22 to 30‰.

TABLE 1.—List of fishes and common macroinvertebrates that were associated with the subtidal patches of oyster shells in Georgia.

Polychaete worm	Shrimps
Nereis succinea	*Palaemonetes vulgaris*
	Palaemonetes pugio
Snails	Crabs
Urosalpinx cinerea	*Callinectes sapidus*
Terebra dislocata	*Menippe mercenaria*
Odostomia sp.	*Rhithropanopeus harrisi*
	Neopanope texana sayi
Bivalves	*Eurypanopeus depressus*
Petricola pholadiformis	*Panopeus herbstii*
Brachidontes exustus	*Pagurus longicarpus*
	Fishes
Isopods	*Gobiosoma bosci*
Sphaeroma quadridentatum	*Gobiosoma ginsburgi*
Cassidinidea lunifrons	*Gobiesox strumosus*
	Opsanus tau
Amphipods	*Hypsoblennius hentzi*
Gammarus sp.	*Chasmodes bosquianus*
Melita nitida	*Hypleurochilus geminatus*

ASSOCIATED SPECIES IN OYSTER PATCHES

Other fishes and conspicuous invertebrates were collected with the gobies for the purpose of characterizing the small oyster shell patches and to allow comparison with the larger, typical oyster reefs. The larger reefs are primarily intertidal in sounds and high-salinity rivers. The small reef patches are mostly subtidal and are subjected to a stronger ebb tide current and probably more erosion than the larger reefs in the mud flats.

Most of the invertebrates and all the fishes collected (Table 1) were reported for North Carolina oyster reefs by Wells (1961). The only records we add are the amphipod *Melita nitida* and the auger *Terebra dislocata*. Some species that we consider to be common in the subtidal reef patches were considered to occur in less than 20% of the collections in North Carolina (Wells, 1961). These include *Palaemonetes pugio, P. vulgaris, Callinectes sapidus, Menippe mercenaria, Rhithropanopeus harrisi, Pagurus longicarpus,* and *Cassidinidea lunifrons.*

The seven species of fishes (Table 1) are characteristic oyster reef species. They are intimately associated with the reefs. They remain within the interstices of the reef throughout the tidal cycle during the warmest months and all nest there to some degree. However, they become scarce or absent on the reefs in winter. Other fishes collected with oysters (Wells, 1961)

are temporary visitors, do not lay adhesive eggs in the shells, and are rarely found in the interstices of the reef.

The oyster association offers advantages to the gobies and other fishes. The reef provides nesting sites, food, and added protection from predators. A great diversity of reef invertebrates is available for food (Wells, 1961). *G. bosci* eat *Gammarus* and other crustaceans, annelids, small fish, ova (Hildebrand and Schroeder, 1928), and dying oysters (Hoese, 1964). They eat brine shrimp in aquariums and probably feed on other zooplankton in nature. *Gobiosoma* species may be significant predators in the food chain of an oyster community, but are probably unimportant as prey species unless their eggs are eaten. Hildebrand and Cable (1938) reported that eggs of *Chasmodes* attached in oyster shells were preyed on by the crab *Eurypanopeus depressus*. We found three *G. ginsburgi* in the stomach of *Urophycis floridanus*. *Gobiosoma* species are reported in the food of predaceous fishes, including several sciaenids (de Sylva et al., 1962; Darnell, 1958; Hoese, see footnote 3), but their secretive habits would protect them from predation when they occupy reefs.

SEXUAL DIMORPHISM

G. bosci and *G. ginsburgi* are sexually dimorphic in their color, body size, and genital papilla. Male *G. bosci* tend to be darker (Breder and Rosen, 1966), and males were observed to turn darker when they were actively defending their nests. Males reach a larger size than females and are generally larger (Tables 2 and 3) as in *G. robustum* (Springer and McErlean, 1961). For *G. bosci*, the largest male and female were 50 mm and 37 mm SL (standard length), respectively. Corresponding lengths of *G. ginsburgi* were 41 and 32 mm. Maximum recorded length of *G. bosci* is 58 mm (Schwartz, 1961). Male *G. ginsburgi* reach 53 mm total length (42 mm SL) (de Sylva et al., 1962).

The sexes are easily separable by the structure of the genital papilla (Ginsburg, 1933). The papilla of males is triangular and compressed, whereas the papilla of females is conical, fleshy, with a larger opening than in males, and with fingerlike projections around the tip. The papilla is poorly developed in juveniles, accounting for most of the unsexed specimens in Tables 2 and 3. The papilla is most developed during the breeding season in *G. robustum* (Springer and McErlean, 1961).

Ginsburg (1933) found a predominance of males in collections of *G. bosci*, *G. ginsburgi*, and *G. robustum* and considered this to be possibly due to gear selectivity for the larger gobies. With the exception of collections of guarded nests, there is a relatively even sex ratio in our collections of *G. bosci* and *G. ginsburgi*. For example, *G. bosci* was represented by 20 males

TABLE 2.—Monthly length frequencies of *Gobiosoma bosci* from the Georgia coast, April 1967-June 1970. M - male, F - female, U - sex unknown (including juveniles), I - incubation of eggs or larvae, G - gravid female. None were collected in September.

Length (mm)	Jan.	Feb.		Mar.		Apr.			May			June			July			Aug.		Oct.	Nov.		Dec.		Total
	F	M	F	M	F	MI	F	U	MI	FG	U	MI	F	U	MI	FG	U	M	U	M	M	F	M	U	
13-15			2											4			3		2					1	12
16-18		2	3											4			4		1						14
19-21		2	8											3							1				14
22-24		5	5		1							1			3			1				2			18
25-27	1	4	4	1	1					1					2										14
28-30	1	4	3					2	2	1		2	1			2			1	1			1		21
31-33		3			1					2		2	1		2	2		2					2		17
34-36		1	1	2		1			3			4			3	1					1				17
37-39		1		1			1		4		2	3			4	1					3				20
40-42		3		2					5		2	7			5										24
43-45						1			3			3			3										10
46-48				1		1						1													3
49-51									1																1
Total	2	25	26	7	3	3	1	2	18	4	4	23	2	11	22	6	7	3	4	1	5	2	3	1	185

TABLE 3.—Monthly length frequencies of *Gobiosoma ginsburgi*, from the Georgia coast, April 1967-June 1970. M - male, F - female, U - unidentifiable sex (including juveniles), I - incubation of eggs or larvae, G - gravid female.

Length (mm)	Jan.			Feb.		Mar.			Apr.			May		June	Aug.	Oct.	Nov.			Dec.	Total
	M	F	U	M	M	F	U	MI	U	MI	FG	U	MI	U	U	M	F	U	U	
8-10															1	1					2
11-13			2																1	1	4
14-16				1	2		1		1												5
17-19					9	8											1	1			19
20-22	1	1		1	5	10					1	1	1								21
23-25		1			8	10			1	2	1										23
26-28	1				9	17				5	1		1								34
29-31					6	8		5		2											21
32-34					4	1		1		3											9
35-37					11					1											12
38-40					4																4
41					1																1
Total	2	2	2	2	59	54	1	6	2	13	3	1	2	1	1	1	1	1	1	1	155

and 25 females in February collections from the tidal creek. March collections of *G. ginsburgi* from burrows in an eroding clay outcrop at Sapelo Beach included 59 males and 54 females. This even sex ratio also occurs in *G. robustum* (Springer and McErlean, 1961).

NESTING BEHAVIOR

G. bosci and *G. ginsburgi* apparently have evolved an instinctive ability to select nesting sites that will allow successful reproduction. They lay adhesive eggs inside dead, gaping, hinged oyster shells, which provide a clean stable substrate and protection from predators. The size of the aperture of the oyster shell, its submergence throughout the tidal cycle, and the amount of water circulation provided by tidal currents seem to be important criteria for selection of nesting sites in reef areas. Though nests were most commonly found in oyster shells, we collected one male *G. bosci* with eggs from a hinged quahog (*Mercenaria mercenaria*) shell. Nelson (1928) also reported *G. bosci* nesting in "clam" shells, and Breder (1942) found nests of the reproductively similar *G. robustum* in sponges and scallop shells.

We noted during our collection of nesting shells that all nests were below mean low tide, and none were found emerged during the extremely low spring tides. The gape of each nesting shell was just large enough to allow the goby to enter. This characteristic gape facilitated our recognition and collection of nests. Closing the shells before extracting them from the reef prevented escape of the parent gobies.

Nests seemed to be located where the tidal current restricted siltation and stagnation at low tide. Masses of developing eggs and larvae probably require a continuous flow of water to provide oxygen and remove metabolic waste products. In aquarium observations, male gobies provided additional circulation by fanning the egg masses with slow undulations of the caudal fin. They apparently display this behavior in nature because all egg masses examined were free of silt.

Male *G. bosci* and *G. ginsburgi* guard and aggressively defend the nest until the eggs hatch and larvae become free-swimming. In laboratory observations males even attacked inanimate objects such as pipettes which were inserted into the nest. In defensive display, the dorsal fin and pelvic disc were erected, the mouth was opened broadly, and the body color was darkened. The erected pelvic disc elevated the body and may function to make the goby appear larger.

Male *G. bosci* were observed to successfully defend their nests against other male *G. bosci* introduced in the vicinity of the nest. Attached eggs of *G. ginsburgi* placed with male *G. bosci* were promptly eaten, even when the males were guarding their own eggs. Furthermore, male *G. bosci* were cannibalistic when presented with unfamiliar unhatched eggs while guarding their own nests. Both species may be important predators on eggs of their own species and other species nesting in oyster reefs. Since we saw

no evidence that males ever eat their own eggs, they apparently are able to distinguish their own progeny or nest from those of other individuals. Male gobies do not fast while incubating eggs. In fact, they temporarily left their nests to feed on brine shrimp (*Artemia*) introduced into aquariums.

SPAWNING SEASON OF *GOBIOSOMA BOSCI*

The spawning season of many marine fishes becomes longer to the south along the U.S. Atlantic coast in relation to warmer waters. Naked gobies spawn in the warmer months and both ends of their spawning season become protracted to the south. In New York waters *G. bosci* probably spawns from June through August (Greeley, 1939; Perlmutter, 1939). Nests of *G. bosci* were found in late May and June in New Jersey (Nelson, 1928). Small *G. bosci* (4-7 mm) occur from June through October in Delaware (de Sylva et al., 1962). Spawning apparently occurs from May through October in Virginia (Massmann et al., 1963; Schwartz, 1961; Hildebrand and Schroeder, 1928). On the Carolina coast spawning is from June to October (Kuntz, 1916; Breder and Rosen, 1966) and possibly beginning in late April or early May (Hildebrand and Cable, 1938). We found *G. bosci* nesting in oyster patches only during the peak of its spawning season in Georgia, from April 24 through July (Table 2). Its spawning season commences in early April in Mississippi and extends to October in Mississippi (Dawson, 1966) and Tampa Bay (Springer and Woodburn, 1960).

The spawning season of *G. bosci* probably ranges from a 3-month period, June-August, in New York to a 6- or 7-month period on the Gulf coast. Mean monthly water temperatures can be used as a rough indication of the relationship of temperature and spawning season; however, these may be somewhat extreme for the months at the beginning and ending of the breeding season. Temperature data are from U.S. Coast and Geodetic Survey (1961) stations at Montauk, Long Island, N.Y.; Breakwater Harbor, Del.; Gloucester, Va.; Southport, N.C.; and Eugene Island, La. Mean temperatures at the beginning and ending of spawning were 16° and 21°C in New York, 20° and 17°C in Delaware, 20° and 19°C in Virginia, 18° (April) or 23° (May) and 26°C in North Carolina, and 20° and 23°C on the central Gulf coast. Spawning commenced at 20°C in New Jersey (Nelson, 1928). Pending more thorough studies of spawning seasons, it can be concluded that spawning of *G. bosci* commences in the spring when water temperatures are 16° to 20°C and terminates in the fall or late summer.

The peak of spawning activity is in the warmest months, May through August, from New York to the Gulf coast. Therefore, this peak is related to temperature seasonally, but it does not change geographically in relation to temperature as Dahlberg (1970) demonstrated for the Atlantic menhaden, although summer maximums (mean monthly temperatures) range from 21°C in New York to 30°C in Louisiana. Higher summer maximums of 30° to 31°C in Tampa Bay apparently suppressed the spawning of a congener, *G. robustum* (Springer and McErlean, 1961).

SPAWNING SEASON OF *GOBIOSOMA GINSBURGI*

Available data indicate that the spawning season of *G. ginsburgi* is very similar to that of *G. bosci*. *G. ginsburgi* probably spawned from July to October in Delaware as 2 to 6-mm larvae were found in these months (de Sylva et al., 1962). One *G. ginsburgi* was ripe in May in Virginia (Hildebrand and Schroeder, 1928). In oyster patches males were incubating nests on April 24 when the shallowwater temperature was 26°C in May and June. An 8-mm specimen dredged in Sapelo Sound on August 28 was probably spawned in August. If spawning continued into the fall as in Delaware, it may be restricted to deep waters since no nests were found after June. The stomach of a *Urophycis floridanus* contained three female *G. ginsburgi* (22-30 mm) that were gravid and appeared to be ready to spawn. The *U. floridanus* was trawled on 1 May 1969 in water depth over 7.6 m in the North Newport River, Liberty

County, Georgia. An abundance of shell on bottom probably would provide a suitable spawning site.

EGG SIZE AND FECUNDITY

To analyze fecundity, eggs were counted in nests and ovaries. Eggs from ovaries of three *G. bosci* and one *G. ginsburgi* were counted and measured (Table 4). Thirty-five to 50 randomly selected eggs from both ovaries were measured with a filar micrometer eyepiece adapted to a 20× dissecting scope. Random egg diameter measurements were made as in Springer and McErlean (1961).

TABLE 4.—Sizes and numbers of eggs from ovaries of *Gobiosoma bosci* and *G. ginsburgi* in Georgia. Two size classes were found in *G. ginsburgi*.

Standard length	Date caught	Diameter of eggs		Number of eggs
		Average	Range	
mm		mm	mm	
G. bosci				
27	19 May 1970	0.195	0.112 - 0.247	701
28	19 May 1970	0.170	0.112 - 0.242	966
35	11 July 1967	0.599	0.526 - 0.720	1,382
G. ginsburgi				
25	1 May 1969	0.154	0.112 - 0.211	
		0.602	0.549 - 0.684	434

In one ripe *G. ginsburgi*, ova of two size classes were equally distributed throughout the ovary. Large ova were 0.55 to 0.68 mm, and small ova were 0.11 to 0.21 in diameter. In *G. robustum* the size range was somewhat greater and ripe ova were 0.476 to 0.782 mm (Springer and McErlean, 1961). The immature eggs may be spawned the following year or not at all. Springer and McErlean concluded that it is possible that sufficient time remains in the fall for the small egg class to be spawned; however, they also observed that the late spawners (mostly in fall) were entirely or mostly of a different year class than the early spawners (mostly in spring). In the fall, females matured at small sizes, 14.6 mm in *G. robustum* and 12.9 in *G. longipala* (Dawson, 1966). In three gravid *G. bosci* we found none of the small size class of eggs in the ovaries.

Springer and McErlean (1961) reported up to 402 eggs in a single ovary and approximately the same number in left and right ovaries of *G. robustum*. Our counts are based on both ovaries. Four nests of *G. ginsburgi* contained 354, 400, 790, and 1,884 eggs. Distinctly different stages of development were apparent in the largest nest. One female *G. ginsburgi* (25 mm) had 435 ripe eggs plus a similar number of immature ova. Fourteen *G. bosci* nests contained 332 to 2,000 eggs and three others had 3,933, 8,000, and over 9,000 eggs. The fact that three gravid females contained only 701 to 1,382 eggs points to a polygamous nature of the males. Further evidence of polygamy is the difference in developmental stages of adjacent egg masses in nests of *G. bosci* and *G. ginsburgi*. This polygamous behavior occurs in a closely related group, *Gobius*, and in an oyster associate, the oyster toadfish, *Opsanus tau* (Breder and Rosen, 1966). However, Runyan (1961) concluded that variation of developmental stages within *Gobiesox* egg clusters probably resulted from deposition on successive days, and she found no evidence for polygamy.

Fishes characteristic of oyster reefs have evolved parallel patterns of reproductive behavior. Adhesive eggs are incubated and guarded by the males. There are various degrees of reliance on oyster shells for nests. The extent of polygamy is not known. Low fecundity is characteristic of fishes that exhibit parental care. We found that egg counts in oyster shells were 319, 1,001, and 2,302 for *Gobiesox* and 1,058, 1,502, and 3,856 for *Chasmodes*. Runyan (1961) found 1,600 eggs in an average-sized female *Gobiesox* and 300 to 2,500 eggs in shells.

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CALORIC MEASUREMENTS OF SOME ESTUARINE ORGANISMS[1]

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ABSTRACT

The caloric content per gram dry weight, per gram ash-free dry weight, and per gram live weight was determined for 51 species of organisms, representing the Ctenophora, Mollusca, Annelida, Arthropoda, Echinodermata, and Chordata, collected from the shallow estuarine system near Beaufort, N.C. Least squares regression analysis showed a highly significant correlation between caloric content per gram dry weight and the percentage organic matter. Decalcification of molluscan tissues did not significantly lower caloric values. We observed significant differences for caloric values of species grouped by phylum, and an evolutionary trend toward increasing energy content per gram live weight. We also observed a frequency distribution of energy which was skewed toward lower values.

Existing publications on the caloric content of organisms (Golley, 1961; Slobodkin and Richman, 1961; Paine, 1964; Cummins, 1967; Brawn, Peer, and Bentley, 1968; Cummins and Wuycheck, 1970) list few species which spend all of or part of their life histories in estuaries. In 1968 we began a survey of the caloric content of estuarine organisms. With knowledge of the caloric content of these species-populations our data on biomass in the shallow system of estuaries near Beaufort, N.C., could be converted to standing crop energy to facilitate the analysis of energy flow in this system. The means for these populations are presented as calories per gram dry weight, per gram ash-free dry weight, and per gram live weight to permit investigators who do not have access to a calorimeter to estimate energy units for their estuarine biomass data.

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METHODS

Organisms were collected in the Newport River estuary and surrounding estuaries near Beaufort. Detailed descriptions of the hydrography of this shallow estuarine system are presented by Williams (1966), Williams and Murdoch (1966), and Thayer (1969). The Newport River has a mean depth of 1.2 m, and the water column generally lacks vertical stratification. Salinity and temperature range from 13 to 35‰ and 7° to 32°C. The sediments of this estuary are primarily of shell and sand near the ocean with finer sands, clays, and silts predominating toward the mouth of the river.

Organisms were processed promptly after collection. All organisms, except ctenophores, were rinsed with distilled water, blotted, and weighed. Ctenophores were rinsed with distilled water and weighed intact without blotting. Gut contents of all organisms were included in the analyses, and this may have accounted, especially in the case of ctenophores, for some of the variability in caloric measurements. Meats were removed from the larger molluscs by shucking and from the smaller molluscs by decalcification with 20% HCl. Decalcification normally required 2-4 min,

after which the meat and shell matrix were removed, rinsed with distilled water, blotted, and dried. The majority of organisms and molluscs meats were dried in a lyophilizer and ground to pass through a 40-mesh sieve. Samples collected during 1968 were dried at 60°C in an oven; no attempt was made to compare the results of caloric measurements on freeze-dried and oven-dried samples.

Caloric determinations were made with a Phillipson type oxygen microbomb calorimeter (Gentry Wiegert Instruments).[4] Three to eight pellet replicates, weighing from 5 to 25 mg dry weight each, were run for each sample. After each combustion a nitric acid determination and correction was made (Parr Instrument Co., 1960). In addition, sulfur content of each sample was determined (American Public Health Association, 1965) and a sulfur correction was made on each replicate. Subsamples of each material were ashed in a muffle furnace at 500°C for 36 hr. Caloric content on a dry weight and an ash-free dry weight basis were calculated according to the Parr Manual (Parr Instrument Co., 1960) and Phillipson (1964).

RESULTS AND DISCUSSION

We combusted 425 pellets of 93 samples representing 51 species-populations collected from the estuarine system near Beaufort. The values we obtained for ash content, percent dry weight, and caloric content based on dry weight, ash-free dry weight, and live weight are presented in Appendix Table 1. Some general conclusions have emerged from calorimetric studies, with which our data agree, but specific values and relations for an estuarine system have not been presented before.

We observed a statistically significant relation between energy content per gram dry weight and the percent of organic matter in the sample ($r = 0.857$; $d.f. = 91$) (Figure 1). The least squares regression equation was

$$Y = 0.0604X - 0.420,$$

where Y is kilocalorie per gram dry weight and X is the percent organic matter (ash-free dry weight) in the sample. This equation is similar to those obtained by chemical composition techniques (Ostaypenya and Sergeev, 1963) for marine and freshwater organisms:

$$Y = 0.0616X - 0.286$$

and for marine crustaceans and molluscs:

$$Y = 0.0617X - 0.531.$$

The similarity of the three regression equations suggests a general relation between the caloric content and the percent dry matter of all aquatic organisms. We are continuing to collect and analyze samples, however, to determine whether there are seasonal differences.

The linear regression suggests that if there are changes in chemical composition of the organic matter, primarily differences in the percent lipid material, they are obscured in this relation by relatively large amounts of inorganic substances in the dry tissues of the organisms. We therefore analyzed the correlation between energy content per gram organic matter and the percent organic matter in the samples. Where applicable, corrections for endothermy (Paine, 1964, 1966) were applied. The resulting correlation, although significant, was low ($r = 0.333$; $d.f. = 91$) indicating great scatter about the regression line. The least squares regression equation was:

$$K = 0.0183X + 3.991,$$

where K is kilocalorie per gram organic matter and X is the percent organic matter. The slope of this line is significantly greater than zero, indicating that the organic matter of the species tested did not have a constant proportion of lipid, protein, and carbohydrate materials. These chemical differences were not obvious from the regression analysis of energy per gram dry weight because they were masked by inorganic substances.

It is possible that acid digestion of molluscs may have altered their caloric content. Paine

[4] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service, NOAA.

(1966) stated that acid digestion would reduce the ash content and the endothermal effect but that the influence of this treatment on the caloric content of the treated samples is not known. Richards and Richards (1965) found small amounts of organic carbon were lost from *Nassarius trivittatus* during decalcification, and this would cause some loss of energy from the samples. Since the majority of gastropods and some of the pelecypods analyzed were decalcified prior to analysis (Appendix Table 1), we analyzed the effect of decalcification on the caloric content of eight sets of mollusc tissues, including three sets of *Modiolus demissus* from Virginia, North Carolina, and Georgia (Table 1).

To determine the maximum effect of decalcification larger organisms were decalcified for a longer period of time than in the routine analysis. Twelve organisms of each set were shucked and one-half of each group was placed in 20% HCl for 15 min (3-8 times longer than for routine analysis of small molluscs). All samples were then dried in a lyophilyzer, and the ash content of the dried material was measured after combustion for 36 hr in a muffle furnace at 500°C. Although decalcification generally tended to reduce the caloric values, in two cases, *Modiolus demissus* (from Virginia) and *Tagelus plebeius*, differences between untreated and decalcified tissue caloric values were significantly different at the 5% level (Table 1). These data suggest that although the shorter decalcification time employed in routine analysis may have lowered the caloric content of the molluscs through protein hydrolysis and extraction of carbon, the decrease probably was insignificant and would not have appreciably affected the regression equation.

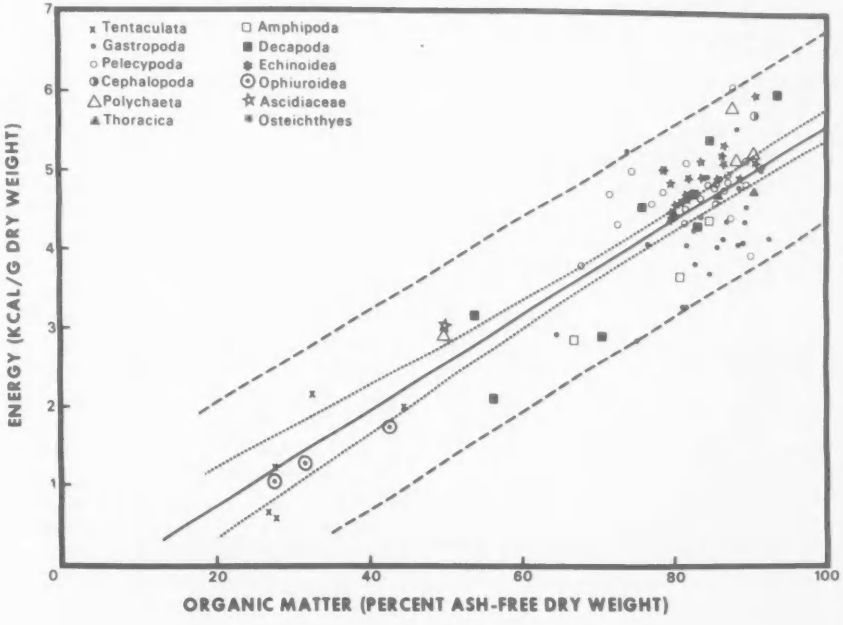

FIGURE 1.—Relation between the caloric and organic content of estuarine organisms. Solid line is the linear regression line; dashed line represents the 95% confidence limits for the prediction equation; dotted line represents the 95% confidence limits for the regression line.

TABLE 1.—Summary of changes in ash and caloric content of decalcified and nontreated tissues of some estuarine molluscs. In each case, six organisms were combined and six caloric measurements made for each combined sample. HCl treatments were for 15 min.

Organism	Collection area	Treatment	Ash %	kcal/g ash-free dry weight	± Standard deviation
Brachidontes recurvus	Florida	None	11.8	5.232	0.056
		HCl	2.5	5.034	0.081
Chione cancellata	North Carolina	None	10.5	5.817	0.096
		HCl	3.7	5.754	0.081
Mercenaria mercenaria	North Carolina	None	18.3	5.235	0.185
		HCl	11.1	5.282	0.045
Modiolus demissus	Virginia	None	11.9	5.036*	0.010
		HCl	3.6	4.783*	0.085
Modiolus demissus	North Carolina	None	15.7	5.118	0.046
		HCl	6.3	4.998	0.087
Modiolus demissus	Georgia	None	5.4	5.102	0.051
		HCl	4.8	5.053	0.095
Mytilus edulis	Virginia	None	13.5	5.006	0.046
		HCl	3.3	5.068	0.045
Tagelus plebeius	North Carolina	None	16.5	5.471*	0.104
		HCl	12.6	4.751*	0.166

*Significantly different at the 0.05 level.

Significant differences in energy content between phyla were observed on the basis of ash-free dry weights and live weights. The phyla show an orderly phylogenetic progression of energy content only on the basis of live weight (Table 2). This is partially the result of decreasing water content of more structurally advanced phyla; we observed significant differences among phylum means for water content which followed a similar trend. Not all phylum means were significantly different, however. The significant overall phylum effect can be attributed to ctenophores' having a significantly lower energy content than the annelids, arthropods, and chordates, but there are no significant differences among the foregoing three phyla nor among the ctenophores, echinoderms, and molluscs (Table 2). Also, within the phylum Mollusca and the class Crustacea the more advanced or more specialized groups (Cephalopoda and Decapoda) had significantly higher caloric contents per gram live weight than the less advanced groups. Although the values we obtained in this study may have resulted from a fortuitous selection of organisms, we feel that the species analyzed are representative of their phyla and that the relation between caloric content, percent dry weight, and percent organic matter, and the phylogenetic position reflects an evolutionary trend for increased caloric content per gram live weight as a result of increased proportion of living tissue with increasing phylogenetic position.

TABLE 2.—Analysis of variance of energy content, in kilocalorie per gram live weight, for all species examined, and listed in Appendix Table 1, and the mean kilocalorie per gram live weight for each taxon.

Source of variation	Degrees of freedom	Mean square	*F* ratio
Among phyla	5	2.494	34.01**
Within phyla	87	0.073	
Total	92	2.567	

Phylum	Mean kcal/g live weight
Ctenophora	0.049
Mollusca	0.373
Echinodermata	0.393
Annelida	0.850
Arthropoda	1.027
Chordata	1.156

**Significant at the 0.01 level.

The differences in caloric content may have arisen from variation in the growth or reproductive stage, or the energy content of the food source. The ctenophores and gastropods showed differences of as much as 1 kcal/g between sampling periods (Appendix Table 1, columns C and D). The variation in the gastropods may have

been the result of increased lipid content prior to spring spawning. We feel that the large variation observed for the ctenophores was partially the result of high energy food in the gut contents. February and March are periods of high zooplankton abundance in the Newport River estuary, and ctenophores may exert heavy predation pressure on zooplankton (Hyman, 1940; Herman, Mihursky, and McErlean, 1968). Consequently, high energy zooplankton (Comita and Schindler, 1963) in the gut may have caused the high caloric values obtained during this period.

The Osteichthyes showed trends in their caloric content which were associated with life history stages and feeding habits. Adult fishes did not show the temporal variation in caloric values which was observed for many of the other taxonomic groups (Appendix Table 1). Postlarval and juvenile stages generally had higher caloric (per unit dry weight and per unit ash-free dry weight) and lower ash contents than their adult stage. The higher caloric content per unit dry weight is of course partly due to the lower ash content. The higher caloric content per unit ash-free dry weight is probably the result of consumption of high energy food such as zooplankton (Comita and Schindler, 1963) by postlarval and juvenile fishes. Adult *Brevoortia tyrannus*, a planktonic feeder, tended to have have higher (but not significant) caloric values (mean 6.018 kcal/g ash-free dry weight) than adult carnivore-omnivore feeding types (mean 5.748 kcal/g ash-free dry weight). The higher values obtained for menhaden are not surprising since up to 28.7% of the wet weight of these fishes may be fats (Perkins and Dahlberg, 1971).

On the basis of limited data Slobodkin and Richman (1961) argued that the frequency distribution of energy (per gram ash-free dry weight) in a "haphazard collection of species" is skewed right, i.e., the modal frequency is at the lower end of the energy range. They explain this distribution by stating that ". . . there has always been selection for maximum number of reproducing progeny, but only sporadic selection for high energy content/gm." Even if there always has been selection for maximum number of reproducing progeny, the analysis of energy content relative to spawning time will affect the results. The argument also ignores the evolution of other life history strategies resulting in fewer offspring with higher survival rates (Mac Arthur and Wilson, 1967; Gadgil and Bossert, 1970) where there may be long-term storage of energy in individual organisms. Cummins and Wuycheck (1970) presented a frequency distribution similar to that of Slobodkin and Richman (1961) and stated that the distribution resulted from the predominance of plant values in their data. We suggest, with Paine (1964), that it may have been premature for Slobodkin and Richman to recognize a particular type of distribution. By combining the results of 15 species of invertebrates with Slobodkin and Richman's data on 17 species, Paine observed a more symmetrical distribution.

If, as indicated by our samples, there is an evolutionary trend toward increased energy content, the predominance of structurally more advanced species in our sample would result in a frequency distribution skewed left as shown in Figure 2. The predominance of advanced species in our samples is consistent with available check lists for the Beaufort area (Duke University Marine Laboratory, 1953; Turner and

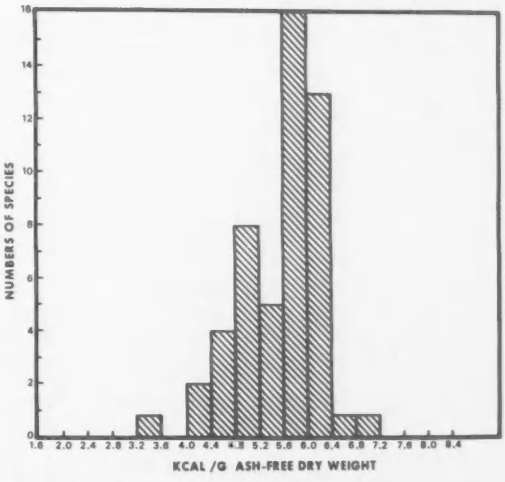

FIGURE 2.—Frequency distribution of energy in a system of shallow estuaries. The values are means for the 51 species presented in Appendix Table 1.

Johnson).[5] The mean of the distribution is 5.57 kcal/g ash-free dry weight, the median is 5.74 and the mode is 5.80. We are continuing to obtain caloric data on these and other species throughout the year to determine whether the frequency distribution of energy in organisms from the Newport River estuary is continually skewed left (Figure 2) or because of seasonal variations follows some other pattern, such as the normal distribution suggested by Paine (1964).

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APPENDIX TABLE 1.—Summary of data collected during caloric analysis of estuarine organisms.

Classification	Collection date	Combustions	(Col. A) Ash	(Col. B) Dry/ live wt	(Col. C)	(Col. D) Energy content	(Col. E)
		Number	%	%	*kcal/g dry wt*	*kcal/g ash-free dry wt*	*kcal/g live wt*
Ctenophora							
Class Tentaculata							
Mixed ctenophores	12-10-69	4	73.2	2.3	[1]0.652 ± 0.419	2.428 ± 1.563	0.014
Mixed ctenophores	1-10-70	6	72.5	2.7	0.579 ± 0.188	1.934 ± 0.546	0.016
Mixed ctenophores	1-22-70	4	72.7	2.8	1.210 ± 0.102	4.439 ± 0.373	0.082
Mixed ctenophores	2-5-70	4	55.5	3.9	2.000 ± 0.103	4.490 ± 0.224	0.079
Mixed ctenophores	3-17-70	4	67.6	2.4	2.178 ± 0.344	6.725 ± 1.062	0.054
Mean			68.3	2.8	1.324	4.003	0.049
Mollusca							
Class Gastropoda[2]							
Bittium varium	11-20-69	6	15.3	10.2	3.696 ± 0.111	4.357 ± 0.119	0.377
B. varium	12-17-69	5	16.4	9.1	4.414 ± 0.199	5.279 ± 0.236	0.402
B. varium	2-11-69	4	23.5	12.2	4.087 ± 0.129	5.334 ± 0.177	0.499
Mitrella lunata	11-20-69	5	18.3	14.8	3.274 ± 0.105	4.005 ± 0.127	0.485
M. lunata	1-14-70	5	7.7	16.1	4.139 ± 0.156	4.483 ± 0.169	0.666
M. lunata	2-11-70	4	10.6	12.5	4.533 ± 0.248	5.060 ± 0.286	0.567
Nassarius obsoletus	11-7-69	4	10.9	9.7	4.096 ± 0.098	4.595 ± 0.111	0.397
N. vibex	1-21-69	4	14.3	6.2	4.027 ± 0.123	4.698 ± 0.145	0.250
N. vibex	11-20-69	3	23.9	6.3	2.855 ± 0.110	3.752 ± 0.144	0.180
N. vibex	2-11-70	3	11.4	5.5	4.805 ± 0.091	5.425 ± 0.098	0.264
N. vibex	3-19-70	4	11.8	4.6	5.575 ± 0.123	6.319 ± 0.139	0.258
Anachis avara	10-29-69	3	18.9	7.3	3.288 ± 0.042	4.108 ± 0.147	0.240
A. avara	12-17-69	4	17.2	7.5	3.816 ± 0.175	4.583 ± 0.214	0.286
A. avara	1-14-70	4	13.8	6.5	4.158 ± 0.153	4.816 ± 0.200	0.270
A. avara	2-11-70	4	17.7	7.8	4.208 ± 0.222	5.099 ± 0.275	0.328
Crepidula convexa	12-17-69	3	35.7	8.8	2.908 ± 4.263	4.553 ± 0.410	0.256
C. fornicata	12-17-69	5	18.4	7.3	4.066 ± 0.132	4.981 ± 0.161	0.297
C. fornicata	4-15-70	4	15.4	6.0	4.957 ± 0.213	5.858 ± 0.252	0.272
C. fornicata (eggs)	4-15-70	4	36.5	7.8	5.248 ± 0.142	8.269 ± 0.223	0.408
Pyramidella fusca	1-14-70	3	11.7	8.6	4.081 ± 0.382	4.621 ± 0.432	0.351
P. fusca	2-11-70	4	26.1	4.0	5.287 ± 0.249	7.158 ± 0.339	0.211
Retusa canaliculata	1-14-70	3	10.7	7.8	4.357 ± 0.281	4.880 ± 0.314	0.340
R. canaliculata	2-11-70	4	8.8	6.2	5.014 ± 0.128	5.491 ± 0.147	0.311
R. canaliculata	3-19-70	4	8.8	5.9	5.072 ± 0.041	5.514 ± 0.044	0.314
Urosalpinx cinerea	2-11-70	3	13.0	4.6	4.369 ± 0.057	5.623 ± 0.060	0.201
Mean			16.7	[3]8.1	4.253	5.154	0.337
Class Pelecypoda							
Pecten irradians	1-14-70	4	12.1	6.0	6.106 ± 0.050	6.949 ± 0.052	0.366
Mercenaria mercenaria	1-2-69	7	25.4	3.1	5.040 ± 0.279	6.757 ± 0.374	0.156
M. mercenaria	12-17-69	5	13.4	3.8	4.793 ± 0.229	5.535 ± 0.264	0.182
Chione cancellata	1-2-69	5	14.4	4.4	4.886 ± 0.150	5.668 ± 0.216	0.215
C. cancellata	12-17-69	3	16.4	4.5	4.699 ± 0.141	5.623 ± 0.169	0.211
C. cancellata	2-11-70	4	18.8	7.7	4.369 ± 0.176	5.381 ± 0.221	0.336
C. cancellata[2]	3-19-70	3	10.5	[3]3.3	5.152 ± 0.072	5.754 ± 0.081	0.170
Tagelus divisus	4-25-69	6	12.2	12.3	4.414 ± 0.442	5.027 ± 0.504	0.543
Modiolus demissus	1-10-69	6	13.0	12.0	5.014 ± 0.342	5.765 ± 0.393	0.601
Crassostrea virginica	12-30-68	6	21.9	3.7	4.756 ± 0.235	6.090 ± 0.301	0.176
C. virginica	4-3-69	6	22.9	3.2	4.605 ± 0.308	5.973 ± 0.400	0.147
Anomia simplex	1-14-70	2	13.0	5.8	4.922	5.660	0.285
Teredo navalis	12-24-69	3	14.4	24.4	4.826 ± 0.079	5.639 ± 0.093	1.178
T. navalis	1-14-70	4	14.8	22.7	4.859 ± 0.165	5.703 ± 0.192	1.069
Macoma balthica[2]	1-14-70	3	10.0	[3]9.9	3.955 ± 0.146	4.391 ± 0.168	0.392
M. balthica[2]	2-11-70	4	18.2	[3]9.0	4.558 ± 0.119	5.776 ± 0.151	0.410
M. tenta[2]	2-11-70	4	27.2	[3]9.2	4.320 ± 0.020	5.935 ± 0.039	0.397
M. tenta[2]	3-19-70	4	28.3	[3]8.2	4.738 ± 0.085	6.611 ± 0.119	0.389
Pinna serrata	3-19-70	4	18.9	8.9	5.129 ± 0.200	6.322 ± 0.247	0.456
Anadara transversa	2-11-70	4	14.9	4.2	4.612 ± 0.134	5.425 ± 0.157	0.194
A. transversa	3-19-70	4	10.3	3.5	4.884 ± 0.088	5.462 ± 0.098	0.171
Mean			16.7	8.1	4.792	5.783	0.383
Class Cephalopoda							
Loligo brevis	12-31-68	5	9.4	18.3	5.743 ± 0.359	6.342 ± 0.398	1.051

See footnote at end of table.

APPENDIX TABLE 1.—Summary of data collected during caloric analysis of estuarine organisms.—Continued.

Classification	Collection date	Combustions	(Col. A) Ash	(Col. B) Dry/live wt	(Col. C)	(Col. D) Energy content	(Col. E)
		Number	%	%	*kcal/g dry wt*	*kcal/g ash-free dry wt*	*kcal/g live wt*
Annelida							
Class Polychaeta							
Amphitrite ornata	1- 2-69	7	50.7	25.4	2.912 ± 0.311	5.906 ± 0.616	0.303
Diopatra cuprea	4-28-69	6	11.9	25.4	5.176 ± 0.433	5.878 ± 0.492	1.315
Nereis pelagica	11-20-69	3	12.2	16.6	5.854 ± 0.128	6.671 ± 0.144	0.972
N. pelagica	2-11-70	3	9.5	15.4	5.252 ± 0.184	5.827 ± 0.204	0.808
Mean			21.1	20.7	4.798	6.070	0.849
Arthropoda							
Order Thoracica[2]							
Balanus balanoides	12-24-69	5	14.1	10.2	4.715 ± 0.235	5.326 ± 0.275	0.481
B. balanoides	1-14-70	5	9.6	10.4	4.777 ± 0.242	5.273 ± 0.278	0.497
Mean			11.8	[3]10.3	4.746	5.299	0.489
Order Amphipoda							
Carinogammarus mucronatus	10-29-69	4	19.4	26.7	3.694 ± 0.322	4.582 ± 0.400	0.986
C. mucronatus	2-11-70	4	15.5	24.7	4.397 ± 0.054	5.202 ± 0.057	1.086
Amphithoe longimana	11-20-69	4	33.3	31.4	2.909 ± 0.188	4.358 ± 0.281	0.913
A. longimana	1-14-70	6	32.3	31.6	3.820 ± 0.209	5.647 ± 0.309	1.207
Mean			25.1	[4]28.6	3.705	4.947	1.048
Order Decapoda							
Paleomonetes pugio	12-31-68	6	15.3	27.4	5.416 ± 0.424	6.393 ± 0.501	1.484
Callinectes sapidus—adult	1-22-69	6	46.4	32.6	3.202 ± 0.375	5.974 ± 0.693	1.044
C. sapidus—immature	11-20-69	5	29.9	27.2	2.945 ± 0.251	4.204 ± 0.358	0.801
Pinnotheres ostreum	4- 8-69	6	6.5	18.5	6.034 ± 0.277	6.357 ± 0.303	1.116
Penceus setiferus	11- 4-69	6	17.7	23.3	4.735 ± 0.163	5.751 ± 0.197	1.103
Callianassa stimpsoni	11-20-69	6	17.1	26.3	4.249 ± 0.113	5.128 ± 0.135	1.117
Upogebia affinis	3-27-69	6	24.4	26.7	4.597 ± 0.376	6.080 ± 0.488	1.227
Libinia dubia	1-14-70	5	44.0	61.9	2.123 ± 0.200	3.215 ± 0.302	1.314
Mean			25.2	[4]30.5	4.163	5.388	1.151
Echinodermata							
Class Echinoidea							
Arbacia punctulata—meat	1-20-69	6	21.6	1.0	5.031 ± 0.467	6.416 ± 0.597	0.050
Class Ophiuroidea							
Ophioderma brevispina	11-20-69	1	72.5	52.3	1.043	3.797	0.551
O. brevispina	1-14-70	4	57.3	32.5	1.763 ± 0.255	4.601 ± 0.667	0.573
O. brevispina	3-19-70	4	68.7	30.7	1.289 ± 0.155	4.438 ± 0.532	0.397
Mean			66.2	38.5	1.365	4.279	0.507
Chordata							
Class Ascidiacea							
Mogula manhattensis	1- 3-69	6	50.3	7.3	3.002 ± 0.332	6.039 ± 0.668	0.219
Class Osteichthyes							
Lagodon rhomboides—adult	12-17-68	7	18.3	26.7	4.665 ± 0.126	5.709 ± 0.153	1.245
L. rhomboides—adult	11-25-69	7	20.6	24.5	4.399 ± 0.308	5.543 ± 0.388	1.078
L. rhomboides—post larval	1-14-70	4	9.2	11.2	6.001 ± 0.420	6.418 ± 0.422	0.672
Brevoortia tyrannus—adult	1-14-70	5	13.7	30.9	5.376 ± 0.210	6.112 ± 0.238	1.661
B. tyrannus—adult	1-22-70	5	13.9	30.2	5.202 ± 0.094	5.925 ± 0.107	1.571
B. tyrannus—post larval	4-22-69	6	9.2	18.5	5.128 ± 0.365	5.694 ± 0.454	0.949
Fundulus heteroclitus—adult	12-24-68	5	19.8	28.5	4.589 ± 0.109	5.722 ± 0.135	1.308
F. majalis—adult	12-17-69	5	20.7	30.2	4.880 ± 0.102	6.155 ± 0.132	1.474
Paralichthys dentatus—adult	8-21-69	7	16.3	23.3	4.927 ± 0.295	5.427 ± 0.345	1.148
P. dentatus—immature	1-14-70	4	11.3	20.7	4.953 ± 0.130	5.588 ± 0.144	1.025
Leiostomus xanthurus—adult	11-25-69	5	16.5	23.9	5.139 ± 0.126	6.152 ± 0.150	1.228
L. xanthurus—adult	5-28-69	5	18.0	22.1	4.948 ± 0.192	6.035 ± 0.234	1.094
Micropogon undulatus—adult	5-28-69	6	19.3	23.7	4.638 ± 0.184	5.744 ± 0.226	1.099
Mugil cephalus—adult	2-27-69	4	20.2	28.3	4.487 ± 0.196	5.393 ± 0.237	1.270
M. cephalus—post larval	1-22-70	2	13.7	24.8	5.142	5.959	1.275
Gobiosoma bosci—adult	10-29-69	4	19.4	32.1	4.758 ± 0.207	5.900 ± 0.256	1.527
Symphurus plagiusa—adult	11- 6-69	6	20.5	22.6	4.492 ± 0.120	5.650 ± 0.138	1.015
S. plagiusa—post larval	11- 6-69	6	14.5	22.5	4.904 ± 0.143	5.735 ± 0.171	1.103
Mean			16.4	24.7	4.924	5.826	1.208

[1] Mean ± 1 standard deviation.
[2] Decalcified with 20% HCl.
[3] Dry weight from dry weight of meat plus protein matrix of shell.
[4] Includes carapace.

NOTES

ATLANTIC THREAD HERRING (*OPISTHONEMA OGLINUM*) - MOVEMENTS AND POPULATION SIZE INFERRED FROM TAG RETURNS

Atlantic thread herring, *Opisthonema oglinum* (Lesueur), occur from Massachusetts southward along the Atlantic coast of the United States, throughout the Gulf of Mexico, and into the Caribbean (Berry and Barrett, 1963; Reintjes and June, 1961). In the South Atlantic area this species is occasionally caught by purse seine vessels fishing for menhaden, *Brevoortia tyrannus*. In the period 1968 through 1970 the catch of thread herring in the South Atlantic averaged 2,000 metric tons. Thread herring have been considered a potential supplement to the declining menhaden catch on the Atlantic coast, although very little is known about population size, distribution, or movement of this species.

The primary objective of this study was to determine if the thread herring population is large enough and is distributed widely enough to provide an alternate resource for the Atlantic menhaden fishery. In September 1968, we tagged 1,582 thread herring about 1 mile off the North Carolina coast: 299 approximately 2 miles west of Beaufort Inlet and 1,283 approximately 5 miles east of Bogue Inlet (Figure 1).

Tags were recovered on magnets at menhaden processing plants during the manufacture of fish meal. Magnets had been installed earlier at all of the plants for recovery of steel tags placed in menhaden. Primary magnets are located in the plant conveyor system between the fish scrap driers and the scrap storage shed. Almost all tags pass over these magnets the same day fish are processed. Secondary magnets were located at other positions in the conveyor system and may not recover tags until months after the fish are landed when the scrap is ground into meal or is shipped from the plant.

Test tags were placed in dead fish entering the plant to determine recovery efficiences. Each week 100 tags were put into fish at each plant, and recoveries throughout the season from these tests were averaged to determine the plants' recovery efficiency.

FIGURE 1.—South Atlantic coast of the United States showing areas of tag release and recovery.

Recovery Efficiencies

Average recovery efficiencies were calculated for each recovery area by recovery year. The following formula was used to determine recovery efficiency for each test:

$$\text{Recovery efficiency} = \frac{\text{Number of test tags recovered}}{\text{Number of test tags released}}$$

Methods and Materials

The tags and methods currently being used to tag menhaden were applied to thread herring.

A manually operated gun with a magazine holding 100 tags (14 mm × 3 mm × 0.5 mm) was used to insert the tags. Individually numbered tags enabled us to determine species, date, and location tagged, and date and location recovered. The gun was designed so that approximately 5 mm of the tag protruded from its barrel. The incision for inserting the tag was made by pushing the tag through the body wall. By holding the end of the barrel against the fish and depressing the plunger, a tag was inserted approximately 5 mm through the body wall into the body cavity (Figure 2). Tests were not performed to determine tagging mortality. However, experiments on menhaden indicate a tagging mortality—tag shed rate of 10-20% for fish over 110 mm having this tag.[1]

Thread herring were tagged aboard menhaden carrier vessels. Fish were dipped from the purse seine, placed in live boxes (2 ft × 2 ft × 4 ft) supplied with running seawater, tagged, and immediately released overboard. Each box held 200-500 thread herring (average 150 mm fork length) for as long as 45 min. Fish did not exhibit overexcitement or die when held in these numbers. Water temperature was 23°C. Average recovery efficiencies and the range of efficiencies are shown for each recovery area by year in Table 1. All recovery efficiencies were calculated from recoveries on primary magnets except the Fernandina Beach, Fla., area in 1968. Only one tag was recovered there on a secondary magnet. Using the average recovery efficiencies, we estimated the total number of tagged fish recaptured from our field tagging (Table 2).

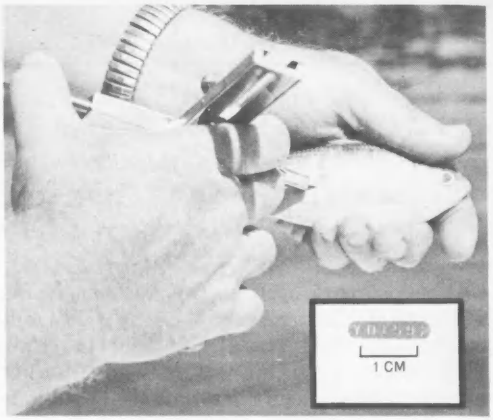

FIGURE 2.—Close-up of thread herring being tagged. Inset: Stainless steel tag.

Movements

Directions of the movements of fish were determined from recaptures of tagged thread herring (Figure 3). In the South Atlantic the menhaden fishing fleets operate near the processing plants, and catches are landed on the same day they are caught. A daily inspection of magnets enabled us to determine the area and date of tag recapture.

In 1968 an estimated 92 tagged fish were recaptured. Twelve of these tagged fish were recaptured near Southport, N.C., about 75 miles south of the release site within 25 days after release. Two months after release, the fish had migrated about 370 miles south to Fernandina

[1] Kroger, R. L., and R. L. Dryfoos. Preliminary tagging and tag-recovery experiments with Atlantic menhaden, *Brevoortia tyrannus*. Manuscript in preparation. National Marine Fisheries Service, Atlantic Estuarine Fisheries Center, Beaufort, NC 28516.

TABLE 1.—Tag recovery efficiencies by year and location where tagged thread herring were recovered, 1968-70.

Recovery year	Recovery location							
	Chesapeake Bay, Va.		Beaufort, N.C.		Southport, N.C.		Fernandina Beach, Fla.	
	Average	Range	Average	Range	Average	Range	Average	Range
	Percent recovery							
1968	No recoveries		52	47-65	67	60-78	33	28-62
1969	67	25-81	49	36-72	77	46-98	22	5-67
1970	No recoveries		No recoveries		70	46-92	No recoveries	

TABLE 2.—Actual and estimated numbers of tagged thread herring recaptured, 1968-70, from 1,582 releases near Beaufort, N.C., September 1968.

Recovery date	Recovery location							
	Chesapeake Bay, Va.		Beaufort, N.C.		Southport, N.C.		Fernandina Beach, Fla.	
	Actual	Estimated	Actual	Estimated	Actual	Estimated	Actual	Estimated
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
1968								
September			39	75				
October			1	2	8	12		
December							1	3
1969								
May					1	1		
July	1	2						
September			7	14	8	11		
October					7	9		
November							2	9
December			1	2				
1970								
October					3	4		

Beach, as indicated by the estimated recapture of three fish there. The Florida recaptures were made prior to November 15, the last day thread herring were caught. The tags were recovered in December on a secondary magnet.

In the spring of 1969 no thread herring were landed. The single recovery in Southport was most likely a holdover from the previous season. There was no offshore spring fishery near Beaufort; thus no possibility of recoveries there.

The recaptures in Chesapeake Bay, Va., came from fish that could have been caught off the northern coast of North Carolina and transported to the Bay as some Chesapeake Bay vessels fished off the North Carolina coast during that period. The plant did not report any thread herring landings, so the thread herring probably were mixed with menhaden.

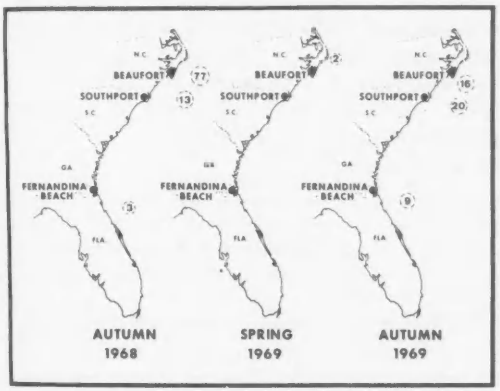

FIGURE 3.—Southerly movements of Atlantic thread herring along South Atlantic coast of the United States, 1968-70.

In the autumn of 1969 tagged thread herring were recaptured sequentially along the South Atlantic coast from Beaufort to Fernandina Beach, again indicating a southerly fall migration. An estimated 16 were recaptured in September at Beaufort, 20 in September and October at Southport, and 9 in December at Fernandina Beach. The December recoveries at Beaufort are the result of tags probably lodged in the conveyor system because thread herring were landed only in September.

In 1970 thread herring were landed only during the autumn. Four fish were estimated recaptured at Southport in October. There was no fishing at Fernandina Beach in late October and November when thread herring are usually caught in that area.

Results from this experiment indicate that thread herring migrate south in the autumn along the South Atlantic coast (Figure 3). Southerly migration rates were estimated from elapsed time and distance between areas. In 1968, about 10 days after release, several tagged fish were recaptured near Cape Fear, N.C., 75 miles south of the tagging site. An additional recapture was made about 370 miles south off

Florida within 53 days after release. The average distance traveled each day from Beaufort to Cape Fear and from Beaufort to Florida was 7.0 miles. In 1969 elapsed time between first recaptures at Beaufort and Florida was 56 days, resulting in an average distance traveled of 6.6 miles per day. From Southport to Florida, the elapsed time was 48 days or 6.1 miles per day. From these recoveries, we estimate that thread herring migrate south in fall at a rate of 6 to 7 miles per day.

Population Size

An estimate of the size of the thread herring population moving south from Beaufort to Southport, in September 1968, can be made using the number tagged (less those recaptured before leaving the Beaufort area), the estimated number recaptured at Southport, and the catch at Southport (Table 3). An estimate of population size from our tagging data requires the assumption that the entire population moves as a group. That assumption is supported by the fact that tagged fish were recaptured with almost all thread herring catches.

For this estimate we are given (Ricker, 1958):

C = Number of thread herring landed at Southport.
M = Effective number of tagged fish at large.
R = Estimated number of tagged fish recaptured at Southport.
$\hat{N}$ = Estimated population size.

then,

$$\hat{N} = \frac{M\,(C+1)}{R+1}$$

or

$$\hat{N} = \frac{(1{,}505)\ (6{,}535{,}583)}{14}$$

$$= 702.6 \text{ million fish} \pm 355.6 \text{ million (95\% confidence interval)}$$

This estimate, made so soon after tagging, could be misleading. No adjustment is possible for the degree of mixing of tagged with untagged fish in the population. Fishing at Southport may have been concentrated on the tagged portion of the population. No adjustment was made for tag loss from shedding and mortality. These effects would produce an underestimate of the stock size. On the other hand, this calculation might overestimate population size because we were unable to determine rate of recruitment.

TABLE 3.—Thread herring landings and estimated number of tags recovered by area from 1968-70.

Area	1968	1969	1970
Chesapeake Bay, Va.			
Number of fish landed	0	[1]0	0
Number tags recovered	0	2	0
Beaufort, N.C.			
Number of fish landed	14,385,394	15,737,303	8,259,404
(metric tons)	(849.4)	(898.6)	(453.4)
Number tags recovered	77	16	0
Southport, N.C.			
Number of fish landed	6,535,582	19,548,161	34,383,824
(metric tons)	(385.9)	(1,116.2)	(1,887.5)
Number tags recovered	13	20	4
Fernandina Beach, Fla.			
Number of fish landed	5,275,548	2,367,776	[2]0
(metric tons)	(311.5)	(135.2)	
Number tags recovered	3	9	0

[1] None of the landings were reported as thread herring.
[2] Fishing terminated early in October before thread herring normally are caught in area.

The one tag recovery from Florida was not used to estimate population size. A single recovery and a low magnet efficiency provide an imprecise estimate of recaptures.

Another estimate can be made using the recoveries and landings from September through November 1969. In this case, sufficient time elapsed for mixing of tagged fish in the population, but tag loss or recruitment were not taken into account. In this estimate:

$$\hat{N} = \frac{(1{,}487)\ (37{,}653{,}241)}{46}$$

$$= 1{,}217.2 \text{ million fish} \pm 355.1 \text{ million (95\% confidence interval)}$$

We feel these estimates, although very gross, are indicative of the population size for the purpose of this study. The catch of thread herring in 1968 was approximately 1,547 metric tons and in 1969 was 2,150 metric tons (Table 2), while in 1968 and 1969 the average catch of men-

haden in the South Atlantic summer fishery alone was 34,435 metric tons.

Estimates of the thread herring population size expressed in metric tons equal approximately 45,000 ± 23,000 in 1968 and 71,000 ± 21,000 in 1969. The 95% confidence intervals suggest that true population size might vary from 22,000 to 92,000 metric tons. Thus, the thread herring resource appears capable of supporting a larger fishery at this time since not more than 10% of the population was harvested in 1968 or 1969, but it does not appear to have the capacity to offer an alternate resource for the Atlantic menhaden fishery. Thread herring distribution is generally limited to the South Atlantic area, whereas Atlantic menhaden are distributed along most of the Atlantic coast of the United States. A 50% harvest rate, at most, would amount to little more than the present menhaden landings in the South Atlantic summer fishery.

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MERISTIC CHARACTERS OF SOME MARINE FISHES OF THE WESTERN ATLANTIC OCEAN[1]

This report presents data on meristic characters from radiographs of 642 species of marine fishes representing 113 families, collected from Cape Hatteras, N.C., to northern Brazil, including the Gulf of Mexico and the Caribbean Sea. Most of the specimens were collected on cruises of the National Marine Fisheries Service. The chartered vessel *Silver Bay* and the NMFS research vessel *Oregon* made these cruises from the Exploratory Fishing and Gear Research Base, Pascagoula, Miss., and the Exploratory Fishing and Gear Research Station, St. Simons Island, Ga. Additional material was obtained from shrimp trawling and beach seining in coastal Georgia. Papers by Hollister (1936, 1937a, b, 1940, 1941), Clothier (1950), Hubbs and Lagler (1958), and Lagler, Bardach, and Miller (1962) were helpful in determining vertebral and other skeletal characters. The phylogenetic arrangement and spelling of families, genera, and species were made, when applicable, in accordance with the American Fisheries Society's *List of Common and Scientific Names of Fishes* (Bailey, 1970).

Methods and Procedures

We x-rayed at least four specimens of most species; for some species fewer than four were available. Specimens ranged from 12 to 580 mm standard length (SL). Specimens smaller than about 60 mm SL were x-rayed with a soft-ray machine and larger specimens with a hard-ray machine.

Counts of precaudal and caudal vertebrae, dorsal and anal spines, and soft rays, and primary and secondary caudal rays were made with the aid of a dissecting microscope or an x-ray illuminator. These meristic counts for all species were made independently by each of us;

[1] Contribution No. 99, National Marine Fisheries Service, Southeast Fisheries Center, Brunswick Laboratory, Brunswick, GA 31520.

we exchanged radiographs and checked each other's work; then at a later date and following the same procedures, we reread the radiographs.

The counts (Table 1) very likely do not represent the complete range for any species because too few specimens have been examined. Counts from specimens with obvious deformities or any recognizable abnormality or aberration are not included. When more than one separate dorsal or anal fin is present, and composed of soft rays only (e.g., Gadidae and Moridae), the count for the anterior fin is followed by a comma and the count for the posterior fin. Dashes are used to separate counts, or to replace counts to indicate that we were unable to make an accurate count from the radiograph.

In the dorsal fin in *Macrozoarces americanus* (Zoarcidae), two groups of soft rays are separated by spines. Finlets in Carangidae, Gempylidae, Scomberesocidae, and Scombridae are separated from fin-ray counts by a plus (+) sign. A plus sign is also used to show a divided anal fin in Sternoptichidae.

Cyclopterus lumpus and *Enchelyopus cimbrius* normally occur north of the study area, but their meristics were available and are included in this paper for comparative purposes. Some species which are anadromous have been included, e.g., *Alosa sapidissima*, even though the adults have been taken only in fresh or brackish waters. Other species, e.g., *Agonostomus monticola*, are reported in the literature as occurring in fresh water only but are included here because at times they have been found in the ocean (Anderson, 1957).

Definitions

In the following definitions we have tried to provide a general scheme for distinguishing the meristic characters of 642 different species although all specimens of all 642 species do not agree with our guidelines.

Total vertebrae: All vertebrae, includes the anteriormost centrum, and the urostyle which we count as the terminal centrum.

Precaudal vertebrae: Vertebrae with no hemal arches or hemal spines.

Caudal vertebrae: Vertebrae with hemal spines; typically the first hemal spine is associated with one or more anterior proximal radial elements of the anal fin. Our definition of precaudal and caudal vertebrae will not work for all species because in certain groups, e.g., Clupeidae, transitional centra may be present. If transitional centra are known to occur, the total number of vertebrae is a more meaningful character than a precaudal and caudal vertebral separation.

Spines: All true spines are median unpaired structures, without segmentation; they are usually stout and rigid with sharp tips and are never branched.

Rays (Soft rays): Are usually, though not always, branched and flexible, and are paired and segmented. Dorsal and anal fin-ray counts include all rays observed. If the terminal ray is bifid and articulated with a single pterygiophore, it is counted as one ray. Dorsal or anal fin spines are tabulated as a group; a spine in the second fin (if a spine is present) is counted with the spines of the anterior fin.

We distinguished caudal primary (principal) soft rays as those which articulate with the hypural bones. Typically the primary rays include all of the branched rays plus one dorsal and one ventral unbranched ray. In some species the primary caudal rays may all be branched. Some species have primary rays only. Primary rays often overlap onto the epural bones or hemal spine of the penultimate vertebra, and our personal judgment, based upon our interpretation of the literature, was used to determine if the ray was primary or secondary (procurrent). In a few species no distinction between primary and secondary rays could be made from the radiograph, and the total number of caudal soft-rays is listed.

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TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.

FAMILY Genus, species	Size range	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	cm	No.	Number											
ACANTHURIDAE														
Acanthurus bahianus	8-9	1	22	9	13	9	27	3	22	28	6	8	8	6
Acanthurus chirurgus	27-110	5	22	9	13	9	23-24	3	21-23	26	5	8	8	5
Acanthurus coeruleus	26- 31	4	22	9	13	9	26-28	3	25	26-27	5	8	8	5-6
ALBULIDAE														
Albula nemoptera	310	1	77	46	31	0	22	0	9	35	8	10	8	7
Albula vulpes	130-170	3	69	42	27	0	18-19	0	8- 9	33	8	10	9	6
ALEPISAURIDAE														
Alepisaurus ferox	105-145	2	50-51	-	-	0	-	0	-	35-38	-	-	-	-
ANOPLOGASTRIDAE														
Anoplogaster cornuta	55- 82	2	25-27	12	13-15	0	16-18	0	9	-	6	-	9	6-7
ANTENNARIIDAE														
Antennarius multiocellatus	41- 60	2	18	10	8	3	12	0	6- 7	9	0	4	5	0
Antennarius ocellatus	57	1	19	10	9	3	13	0	8	9	0	4	5	0
Antennarius radiosus	66- 98	4	19	10	9	3	13	0	8	9	0	4	5	0
Antennarius sanguineus	33	1	19	10	9	3	13	0	7	9	0	4	5	0
Histrio histrio	70- 84	4	18	10	8	3	12	0	7	9	0	4	5	0
Lophichaetus tenebrosus	66	1	18	10	8	4	12	0	7	9	0	4	5	0
Pterophryne histrio	57- 86	3	18	10	8	3	12	0	7	9	0	4	5	0
ARGENTINIDAE														
Glossanodon pygmaeus	62- 88	4	45	23	22	0	10-11	0	10	38-40	9-11	10	9	9-10
Microstoma microstoma	195	1	47	31	16	0	12	0	8	40	11	10	9	10
ARIIDAE														
Arius felis	94-145	4	50-52	22	28-30	1	7	0	18-19	53-55	19-20	7	8	19-20
Bagre marinus	152-164	2	53-54	22	31-32	2	7	0	26-28	58-59	22-23	7	8	21
ASTRONESTHIDAE														
Astronesthes similis	42- 85	4	53-55	37	16-18	0	11-12	0	19-20	32-35	8- 9		9	5- 7
ATELEOPIDAE														
Ijimaia antillarum	220-325	4	127-129	29-31	97-100	0	9	0	82-89	-	-	-	-	-
ATHERINIDAE														
Allanetta harringtonensis	58- 64	4	43-44	22-23	21	7-8	10	1	11	33-36	8- 9	9	8	8-10
Membras martinica	54- 92	3	43	19	24	5	7-8	1	18-19	32-35	7- 8	9	8	8-10
Menidia beryllina	30- 37	4	41-42	18	23-24	5	6-8	1	17-18	-	-	9	8	-
Menidia menidia	28- 57	4	39-41	16-17	23-24	5	7-8	1	21-25	35-38	9-11	9	8	9-10
AULOPIDAE														
Aulopus nanus	133-195	2	48	33	15	0	15	0	11-12	34-35	8- 9	10	9	7
AULOSTOMIDAE														
Aulostomus maculatus	90-225	2	57	21	36	10	28	0	29	20	3	7	7	3
BALISTIDAE														
Alutera heudeloti	89-174	3	20	7	13	2	36-39	0	40-42	12	0	6	6	0
Alutera monoceros	121	1	23	7	16	2	47	0	50	10	0	6	6	0
Alutera schoepfi	95-165	4	23	7	16	2	33-35	0	35-37	12	0	6	6	0
Aluterus scriptus	52-118	4	21	7	14	2	44-47	0	47-49	12	0	6	6	0
Balistes capriscus	155-174	3	18	7	11	3	27-28	0	24-25	12	0	6	6	0
Balistes vetula	105-180	3	18	7	11	3	29-30	0	27-28	18	0	6	6	0
Cantherhines pullus	51- 88	4	19	7	12	2	34-36	0	30-32	12	0	6	6	0
Canthidermis maculatus	49- 87	4	18	7	11	3	24	0	21-22	12	0	6	6	0
Canthidermis sufflamen	59- 98	4	18	7	11	3	26-28	0	23-25	12	0	6	6	0
Monacanthus ciliatus	66- 68	4	19	6	13	2	30-32	0	31-32	12	0	6	6	0
Monacanthus hispidus	72-123	6	19	7	12	2	32-34	0	32-34	12	0	6	6	0
Monacanthus setifer	77-111	9	19	7	12	2	27-30	0	27-31	12	0	6	6	0
Xanthichthys rigmus	40- 65	4	18	7	11	2	29	0	24-25	12	0	6	6	0
BATHYCLUPEIDAE														
Bathyclupea schroederi	109-125	4	31	10	21	1	9	1	18	33-35	8- 9	9	8	8- 9
BATHYPTEROIDAE														
Bathypterois bigelowi	105-113	4	49-51	24-25	25-26	0	12-13	0	8-10	27-29	45	10	9	4- 5
BATRACHOIDIDAE														
Opsanus beta	1'5-158	3	32	10	22	3	24-25	0	21-22	18	2	7	7	2
Opsanus pardus	111-184	2	34	11	23	3	26	0	22	18	2	7	7	2
Opsanus tau	121-180	3	34-35	11	23-24	3	27	0	22-23	18	2	7	7	2
Porichthys porosissimus	82-147	5	44-45	12	32-33	2	36-37	0	33-34	15	2	6	7	0
Thalassophryne maculosa	35- 59	2	26	8	18	2	18	0	16-17	18	2	6	7	1
BELONIDAE														
Ablennes hians	70-350	4	93-95	60-62	33	0	23-25	0	16	25-28	5- 7	7	8	5- 6
Platybelone argalus	171-295	4	71	44-45	26-27	0	13	0	17-19	22-25	2- 5	7	8	5
Strongylura marina	175-188	4	73-74	47-48	25-26	0	15-16	0	18-19	24-25	4- 5	7	8	5
Strongylura notata	186-207	4	58-59	36-37	21-22	0	13-14	0	14-15	25-26	5	7	8	5- 6
Tylosurus acus	121-193	4	91	60-62	29-31	0	23-24	0	20-21	28-29	6- 7	7	8	7
Tylosurus crocodilus	108-235	4	82	54-55	27-28	0	21-22	0	20-21	28-30	6- 7	7	8	7- 8
BERYCIDAE														
Beryx decadactylus	180	1	24	10	14	4	14	4	29	28	5	10	9	4
BLENNIIDAE														
Chasmodes bosquianus	52- 70	4	34-35	10	24-25	11	18-19	2	18-19	18	3	7	8	3
Chasmodes saburrae	41- 86	4	33-34	10	23-24	11	17-18	2	17-18	17-19	2- 3	7	8	2- 3
Entomacrodus nigricans	40- 62	4	34	11	23	13	14-15	2	18	26-27	7	7	8	6- 7
Hypleurochilus geminatus	33- 43	4	32-33	10	22-23	12	14-15	2	16-17	21-23	4- 5	7	8	4- 5
Hypsoblennius hentzi	66- 86	4	32-34	10	22-24	12	15	2	16-17	23-24	5- 6	7	8	5
Hypsoblennius ionthas	85	1	33	10	23	12	15	2	17	23	5	7	8	5
Ophioblennius atlanticus	59- 65	5	33	10	23	12	20	2	21	27-29	7- 8	7	8	7- 8

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRATE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
BOTHIDAE														
Ancylopsetta antillarum	111-200	4	36	10	26	0	62-69	0	51-54	18	1	9	8	0
Ancylopsetta cycloides	107-153	4	34-35	10	24-25	0	65	0	49-51	18	1	9	8	0
Ancylopsetta dilecta	126-154	4	36	10	26	0	72-75	0	54-58	18	1	9	8	0
Ancylopsetta kumperae	110-220	4	36	10	26	0	76-79	0	60-63	18	1	9	8	0
Ancylopsetta microctenus	94-218	4	35	10	25	0	62-71	0	51-55	18	1	9	8	0
Ancylopsetta quadrocellata	69-195	4	37	11	26	0	68-73	0	54-57	18	1	9	8	0
Bothus lunatus	54-232	7	40	10	30	0	91-98	0	72-75	17	0	9	8	0
Bothus maculiferus	132-217	3	39-40	10	29-30	0	91-98	0	72-76	17	0	9	8	0
Bothus ocellatus	70-134	4	35-37	10	25-27	0	79-85	0	61-64	17	0	9	8	0
Chascanopsetta prorigera	133	1	55	16	39	0	115	0	86	17	0	9	8	0
Citharichthys amblybregmatus	105	1	35	10	25	0	81	0	67	17	0	9	8	0
Citharichthys arctifrons	101-110	4	36-37	10	26-27	0	76-84	0	63-67	17	0	9	8	0
Citharichthys cornutus	68-77	4	35-36	9-10	25-26	0	79-82	0	63-65	17	0	9	8	0
Citharichthys dinoceros	80-98	4	37	10	27	0	91-94	0	71-73	17	0	9	8	0
Citharichthys gymnorhinus	47	1	34	10	24	0	74	0	59	17	0	9	8	0
Citharichthys macrops	100-147	4	34-35	10	24-25	0	79-84	0	62-63	17	0	9	8	0
Citharichthys spilopterus	87-229	5	34-35	10	24-25	0	75-80	0	57-61	17	0	9	8	0
Cyclopsetta chittendeni	162-169	4	36-37	10	26-27	0	85-87	0	65-68	17	0	9	8	0
Cyclopsetta fimbriata	152-177	4	36-37	10	26-27	0	82-84	0	62-65	17	0	9	8	0
Engyophrys senta	69-82	4	37-38	10	27-28	0	74-80	0	60-64	17	0	9	8	0
Etropus crossotus	109-120	4	35-36	10	25-26	0	79-82	0	63-66	17	0	9	8	0
Etropus microstomus	83-100	4	34-35	10	24-25	0	76-79	0	56-61	17	0	9	8	0
Etropus rimosus	80-95	4	34-35	10	24-25	0	77-79	0	57-63	17	0	9	8	0
Gastropsetta frontalis	132-186	4	37-38	10	27-28	0	61-64	0	48-51	17-18	0-1	9	8	0
Hippoglossina oblonga	156-211	4	41-42	11	30-31	0	76-82	0	61-67	18-19	1	9	8	0-1
Microlene antillarum	110-129	4	45-46	10-11	35-36	0	105-108	0	80-88	17	0	9	8	0
Microlene atrimana	80-118	2	52-53	11	41-42	0	117-121	0	98-103	17	0	9	8	0
Microlene megalepis	78-90	5	43-44	10	33-34	0	91-93	0	72-74	17	0	9	8	0
Microlene sessilicauda	91-130	4	46-47	10-11	36	0	93-104	0	76-83	17	0	9	8	0
Paralichthys albigutta	105-221	4	37	10	27	0	75-80	0	58-61	18	1	9	8	0
Paralichthys dentatus	137-173	4	41-42	11	30-31	0	87-90	0	66-70	18	1	9	8	0
Paralichthys lethostigma	95-213	4	37	10	27	0	82-90	0	64-71	18	1	9	8	0
Paralichthys squamilentus	161-195	3	38	10	28	0	76-85	0	60-64	18	1	9	8	0
Scophthalmus aquosus	111-120	4	34-36	11	23-25	0	64-71	0	50-54	17	0	9	8	0
Syacium gunteri	92-114	4	34-35	10	24-25	0	74-81	0	60-63	17	0	9	8	0
Syacium micrurum	97-154	4	34-35	10	24-25	0	85-87	0	67-70	17	0	9	8	0
Syacium papillosum	157-228	4	35-36	10	25-26	0	85-91	0	67-72	17	0	9	8	0
Trichopsetta caribbaea	84-156	23	41-43	10-11	31-33	0	95-102	0	75-81	17	0	9	8	0
Trichopsetta melasma	72-207	16	41-43	10-11	31-33	0	98-104	0	80-85	17	0	9	8	0
Trichopsetta ortisulcus	97-117	8	40	10	30	0	91-92	0	70-73	17	0	9	8	0
Trichopsetta ventralis	75-143	18	40-41	10	30-31	0	89-95	0	69-75	17	0	9	8	0
BRANCHIOSTROIDAE														
Malacanthus plumieri	222	1	24	10	14	6	53	1	51	39	12	8	7	12
BREGMACEROTIDAE														
Bregmaceros atlanticus	42-48	4	47-49	13	34-36	0	44-46	0	46-47	31-32	-	-	-	-
CALLIONYMIDAE														
Callionymus agassizi	102-132	4	21	7	14	4	8	0	7	15	3	5	5	2
Draconetta acanthopoma	88	1	23	8	15	3	14	0	13	16	3	6	6	1
Draconetta oregona	70-103	3	23	8	15	3	14	0	13	16	3	6	6	1
CAPROIDAE														
Antigonia capros	44-87	4	22	10	12	8	33-35	3	30-32	19	4	6	6	3
Antigonia combatia	85-115	4	22	10	12	9	28-29	3	26-27	18-19	3-4	6	6	3
CARANGIDAE														
Alectis ciliaris	71-91	4	24	10	14	7-8	19	3	16	35-36	9-10	9	8	9
Caranx bartholomaei	113-140	4	24	10	14	9	25-27	3	22-23	33-34	8-9	9	8	8
Caranx crysos	191-212	4	24	10	14	9	23	3	19-20	33-34	8-9	9	8	8
Caranx hippos	99-104	4	24	10	14	9	19-20	3	16-17	34	9	9	8	8
Caranx latus	51-160	4	24	10	14	9	20-21	3	17	33-34	8-9	9	8	8
Caranx ruber	82-137	4	24	10	14	9	27-28	3	24-26	32-35	8-9	9	8	7-9
Chloroscombrus chrysurus	88-125	4	24	10	14	9	26-27	3	26-27	32-35	8-9	9	8	7-9
Decapterus macarellus	180-195	4	24	10	14	9	32-33+1	3	25-26+1	35-36	9	9	8	9-10
Decapterus punctatus	125-155	4	24	10	14	9	31-33+1	3	26-28+1	35	9	9	8	9
Elagatis bipinnulata	60-90	4	24	10	14	7	25-26+1	2	18+1	34-39	7-11	9	8	10-11
Hemicaranx amblyrhynchus	41-54	2	26	10	16	9	28-29	3	24-25	34-35	9	9	8	8-9
Naucrates ductor	245	1	25	10	15	5	26	3	16	36	11	9	8	10
Oligoplites saurus	140-182	3	26	10	16	6-7	20	3	19-20	32-35	9-10	9	8	6-8
Selar crumenophthalmus	147-166	4	24	10	14	9	24-26	3	21-23	31-33	7-8	9	8	7-8
Selene vomer	94-142	4	24	10	14	9	21-22	3	17-18	32-33	8-9	9	8	7
Seriola dumerili	147-205	4	24	10	14	8	28-32	3	20-21	36-41	9-13	9	8	10-11
Seriola rivoliana	47-235	6	24	10	14	8	29-31	3	29-31	36-42	11-13	9	8	8-12
Seriola zonata	187-245	4	24	11	13	9	35-37	3	20	34-40	8-12	9	8	9-11
Trachinotus carolinus	125-182	4	24	10	14	7	24-25	3	21-22	32-33	8	9	8	7-8
Trachinotus cayennensis	327	1	24	10	14	6	26	3	27	32	8	9	8	7
Trachinotus falcatus	39-68	4	24	10	14	7	19-20	3	16-18	30-31	7	9	8	7
Trachinotus goodei	17-60	4	24	10	14	7	19	3	17-18	31-32	7-8	9	8	7
Trachurus lathami	120-150	4	24	10	14	9	29-31	3	27-28	35-37	9-10	9	8	9-10
Vomer setapinnis	117-160	4	24	10	14	9	21-22	3	16-18	32-34	8-9	9	8	7-8
CARAPIDAE														
Carapus bermudensis	126-165	3	118-122	16	102-106	0	-	0	-	0	0	0	0	0
CENTRISCIDAE														
Macrorhamphosus scolopax	68-115	4	24	8	15	7	10-11	0	18-19	27-28	9-10	4	5	9-10
CENTROPOMIDAE														
Centropomus ensiferus	122-280	3	24	10	14	9	9-10	3	6	36-38	10-11	9	8	9-10
Centropomus unidecimalis	56-168	5	24	10	14	9	10	3	6	37-40	11-12	9	8	9-11
CHAETODONTIDAE														
Chaetodon aya	56-90	4	24	10	14	12-14	17-19	3	14-15	24-25	4-5	9	8	3-4
Chaetodon capistratus	49-67	3	24	10	14	12-13	18-20	3	16-17	23	3	9	8	3
Chaetodon ocellatus	99-130	4	24	10	14	12-13	18-20	3	16-17	23	3	9	8	3
Chaetodon sedentarius	82-99	4	24	10	14	13-14	21-23	3	17-19	22	3	9	8	3
Chaetodon striatus	28-92	4	24	10	14	12	20-21	3	16-17	23-24	3-4	9	8	3
Holacanthus bermudensis	98-140	4	24	10	14	14	18-19	3	18-19	25	4	9	8	4
Holacanthus ciliaris	62-183	3	24	10	14	14	20	3	20	25	4	9	8	4
Holacanthus tricolor	113-173	4	24	10	14	13-14	17-19	3	18-19	25	4	9	8	4
Pomacanthus arcuatus	77-128	4	24	10	14	10	28-29	3	22-23	24-25	4	9	8	3-4
Pomacanthus aureus	236-250	2	24	10	14	9	30-31	3	23-24	23-25	3-4	9	8	3-4
Prognathodes scoleatus	52	1	24	10	14	13	19	3	16	24	4	9	8	3
CHAULIODONTIDAE														
Chauliodus sloanei	145-185	4	50-52	-	-	0	5-6	0	11-12	-	7	10	9	-

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
CHAUNACIDAE														
Chaunax pictus	61-123	4	19-20	12	7-8	1	11-12	0	7	9	0	4	5	0
CHEILODIPTERIDAE														
Apogon aurolineatus	40	1	24	10	14	7	9	2	8	29	6	9	8	6
Apogon binotatus	30-60	3	24	10	14	8	8-9	2	7-8	31-32	7-8	9	8	7
Cheilodipterus affinis	39-54	3	24	10	14	7	9	2	7-9	32-34	7	9	8	5-7
Epigonus occidentalis	103-136	4	25	10	15	8	10	2	9	38-39	10-12	9	8	10-11
Epigonus pandionis	99-112	4	25	10	15	8	9-10	2	9	35-37	9-11	9	8	7-10
Phaeoptyx conklini	34-46	3	24	10	14	8	9	1-2	8	27-31	5-7	9	8	5-7
Phaeoptyx pigmentaria	44	1	24	10	14	7	9	2	8	30	7	9	8	6
Phaeoptyx pseudomaculatus	78-87	4	24	10	14	8	9	2	8	30-32	7-8	9	8	6-7
Phaeoptyx quadrisquanatus	42	1	24	10	14	8	9	2	8	31	7	9	8	7
Synagrops bella	118-160	4	25	10	15	10	9	2	7	35-36	10	9	8	8-9
Synagrops pseudocrolepis	83-89	4	25	10	15	10	10	2	9	41-42	12-13	9	8	12-13
Synagrops spinosa	80-115	4	25	10	15	10	8-9	2	7	35	9	9	8	9
CHLOROPHTHALMIDAE														
Chlorophthalmus agassizi	107-127	7	46-48	18	28-30	0	10-12	0	8	43-46	13-14	10	9	11-13
Parasudis truculenta	135-140	4	39	17	22	0	10	0	8-9	40-42	11-13	10	9	11-13
CLINIDAE														
Labrisomus guppyi	30-57	3	35	11	24	19	10-11	2	18-19	29	8	7	6	8
Labrisomus nuchipinnis	90-110	4	34	11	23	18	12	2	18-19	28-30	8-9	7	6	7-8
Starksia Y-lineata	12-14	2	31	10	21	19	7	2	14-15	-	-	-	-	-
CLUPEIDAE														
Alosa aestivalis	137-215	6	47-51	14-16	33-35	0	17-18	0	18-20	32-34	7-8	10	9	6-7
Alosa mediocris	118	1	54	17	37	0	19	0	22	35	9	10	9	7
Alosa sapidissima	103-121	5	56-57	18-19	37-38	0	18-19	0	19-21	33-34	7-8	10	9	7
Brevoortia gunteri	190	1	44	14	30	0	20	0	21	36	9	10	9	8
Brevoortia patronus	84-170	5	45-46	16	29-30	0	20-21	0	21-23	34-36	8-9	10	9	7-8
Brevoortia smithi	72-82	5	45-46	14-15	30-31	0	19-20	0	21-24	33-35	8	10	9	6-8
Brevoortia tyrannus	140-233	3	48	18-19	29-30	0	20-22	0	21-24	32-35	7-9	10	9	6-7
Clupea harengus	190-247	4	55-57	23-25	32-33	0	17-19	0	17-18	31-41	10-13	10	9	8-9
Harengula clupeidianum	137-215	4	48-50	11-13	35-39	0	13-15	0	32-36	35-37	9-11	10	9	7
Harengula petenense	37-62	7	43-44	11-13	30-32	0	14-16	0	22-24	34-35	9	10	9	6-7
Harengula sauvagi	107-125	5	45-50	15-17	30-34	0	18-21	0	11-12	31-32	6-7	10	9	6
Harengula pensacolae	64-77	4	40-42	12-14	27-29	0	16-18	0	17-18	33-35	8-9	10	9	6-7
Jenkinsia lamprotaenia	27-47	8	36-42	19-21	19-21	0	10-12	0	13-15	23-24	3-4	9	8	3
Opisthonema oglinum	57-192	9	45-49	12-13	32-36	0	20-22	0	20-24	34-35	9	10	9	6-7
Sardinella anchovia	23-29	6	45-47	16	29-31	0	16-19	0	16-17	34	8	10	9	7
CORYPHAENIDAE														
Coryphaena equiselis	77-100	4	33	14	19	0	51-54	0	24-27	40-41	11-12	9	8	12
Coryphaena hippurus	91-130	4	31	13-14	17-18	0	58-60	0	27-28	39-43	11-13	9	8	10-13
CORYPHAENOIDIDAE														
Coelorhynchus carminatus	170-205	2	75-78	12	63-66	0	-	0	-	-	-	-	-	-
Nezumia bairdii	350	1	-	14	-	2	10	0	110	-	-	-	-	-
CYCLOPTERIDAE														
Cyclopterus lumpus	387	1	29	11	18	6	10	0	11	15	3	5	5	2
CYNOGLOSSIDAE														
Symphurus civitatus	108-132	4	47-49	9	38-40	8	90-91	0	73-75	12	0	6	6	8
Symphurus diomedianus	128-181	4	48-49	9	39-40	8	90-92	0	74-76	10-11	0	5	5-6	0
Symphurus marginatus	100-112	4	52-53	9	43-44	0	95-98	0	81-84	12	0	6	6	0
Symphurus minor	45-50	2	43	9	34	0	75-76	0	60	10-11	0	5	5-6	0
Symphurus piger	91-106	4	47-48	9	38-39	8	84-87	0	68-72	12	0	6	6	0
Symphurus plagiusa	121-135	4	46-48	9	37-39	0	86-89	0	70-72	10	0	5	5	0
Symphurus plagusia	147-194	4	50-52	9	41-43	0	94-98	0	78-83	11-12	0	6	5-6	0
Symphurus pusillus	93-115	3	53-54	9	44-45	0	95-99	0	83-85	12	0	6	6	0
Symphurus urospilus	96	1	44	9	35	0	85	0	69	11	0	5	6	0
CYPRINODONTIDAE														
Cyprinodon variegatus	34-54	4	26-27	12	14-15	0	12-13	0	11-12	28-29	-	-	-	-
Floridichthys carpio	48	1	23	9	14	0	11	0	9	31	-	-	-	-
Fundulus grandis	65-111	4	33-35	15-16	18-20	0	11-12	0	11	38-42	-	-	-	-
Fundulus heteroclitus	62-72	4	33-34	14	19-20	0	11-12	0	10-11	38-40	-	-	-	-
Fundulus luciae	17-32	10	31-33	12-13	18-20	0	8-9	0	10-11	33-34	-	-	-	-
Fundulus majalis	30-85	4	34-35	15	19-20	0	13-14	0	10-12	37-40	-	-	-	-
Fundulus similis	44-81	5	35-36	15	20-21	0	12-13	0	11-12	38-40	-	-	-	-
DACTYLOPTERIDAE														
Dactylopterus volitans	110-162	4	22	8	14	-	8	0	6	15	3	5	5	2
DIODONTIDAE														
Chilomycterus schoepfi	60-115	5	18-20	-	-	0	10-12	0	9-11	9	0	4	5	0
Diodon holacanthus	97-125	4	-	-	-	0	12-14	0	12-15	9	0	4	5	0
Diodon hystrix	37-168	3	-	-	-	0	15	0	16	9	0	4	5	0
DIRETMIDAE														
Diretmus argenteus	82-95	4	29-30	13	16-17	0	25-26	0	20-21	29	5	10	9	5
ECHENEIDAE														
Echeneis naucrates	210-268	3	30	14	16	0	34-37	0	32-35	37-40	10-11	9	8	10-12
Echeneis neucratoides	103-137	2	30	14	16	0	37	0	33	40	13	9	8	10
Phtheirichthys lineatus	50-61	2	38-39	18	20-21	0	35	0	35	39	11	9	8	11
Remora remora	74-158	6	27	12	15	0	24-26	0	22-24	39-43	11-13	9	8	11-13
ELEOTRIDAE														
Dormitator maculatus	76-77	2	27	12	15	8	8	1	10	32-33	9	8	7	8-9
ELOPIDAE														
Elops saurus	180-233	4	78-80	55-56	24	0	26-28	0	18-19	36-37	9-11	10	9	7-8
Megalops atlanticus	75-115	3	55-56	33-34	22	0	16	0	24-25	32-33	7	10	9	6-7
EMMELICHTHYIDAE														
Emmelichthyops atlanticus	77	1	26	11	15	11	11	3	9	40	12	9	8	11

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
ENGRAULIDAE														
Anchoa cubana	48-67	3	40-41	21-24	19-21	0	14-15	0	18	32-34	7	10	9	6-8
Anchoa hepsetus	65-75	4	42-43	21-22	20-21	0	16	0	20-22	33-36	7-9	10	9	7-8
Anchoa lyolepis	51-82	3	41-43	21-22	20-21	0	14-15	0	21-22	32-35	7-8	10	9	6-8
Anchoa mitchilli	57-67	4	40-43	19	21-22	0	14-15	0	26-27	35-36	9	10	9	7-8
Anchoa spinifer	117-133	4	42-43	17	25-26	0	15-16	0	38-39	37-39	10-11	10	9	8-9
Anchoa tricolor	95	1	43	22	21	0	15	0	21	30	6	10	9	8
Anchovella lepidentostole	63-70	4	40	19	21	0	14-15	0	22-24	31-36	6-9	10	9	6-8
Anchovella perfasciata	28-35	4	43-44	-	-	0	14	0	-	-	-	10	9	-
Cetengraulis edentulus	117	1	41	20	21	0	16	0	25	35	8	10	9	8
Lycengraulis grossidens	140-145	2	43	20	23	0	15	0	27	35	8	10	9	8
EPHIPPIDAE														
Chaetodipterus faber	48-103	4	24	10	14	9	21-23	3	17-18	27-29	5-6	9	8	5-6
ERACOSTIDAE														
Cypselurus comatus	41-182	4	42	26-27	15-16	0	12	0	7-9	26-28	5-6	7	8	6-7
Cypselurus cyanopterus	49-100	4	44-45	30-31	14	0	12-13	0	9-10	27-29	5-6	7	8	7-8
Cypselurus exsiliens	45-186	8	44-45	30	14-15	0	15	0	10	27-28	5-6	7	8	7
Cypselurus furcatus	58-105	3	45-46	29-31	14-16	0	13-14	0	10	29-33	6-9	7	8	8-9
Cypselurus heterurus	197-228	4	46-47	31	15-16	0	13-14	0	9-10	26-29	5-6	7	8	6-8
Exocoetorhamphus velox	190	1	72	46	26	0	22	0	23	23	4	7	8	4
Exocoetus obtusirostris	157-177	3	44-45	26-27	18	0	14	0	14	26-28	5-6	7	8	6-7
Hemiramphus balao	57-70	4	52-56	38-39	16-17	0	13-14	0	11-13	24-27	5-6	7	8	4-6
Hemiramphus brasiliensis	50-90	4	52-53	35-37	16-18	0	13-15	0	12-13	24-25	5	7	8	4-5
Hirundichthys affinis	121-210	3	45-47	29	16-18	0	10-11	0	11-12	30	6	7	8	9
Hirundichthys rondeleti	212	1	45	29	16	0	12	0	12	28	6	7	8	7
Hyporhamphus unifasciatus	137-173	4	51-52	33-34	17-18	0	14-15	0	16	23-24	4-5	7	8	4
Oxyporhamphus micropterus	100-134	4	50	18-19	31-32	0	14-15	0	15-16	23	4	7	8	4
Parexocoetus brachypterus	97-115	4	39	23	16	0	12	0	13-14	23	4	7	8	4
Prognichthys gibbifrons	30-73	4	43-45	27-29	15-16	0	9-12	0	8-9	26-27	4-5	7	8	7
FISTULARIDAE														
Fistularia petimba	240-420	3	82-83	-	-	0	16	-	15	-	-	-	-	6
Fistularia tabacaria	245-470	2	84-85	-	-	0	15	0	14-15	26	6	7	7	8
GADIDAE														
Enchelyopus cimbrius	137-230	4	51-52	16	35-36	0	45-48	0	37-43	30-34	-	-	-	-
Melanogrammus aeglefinus	285	2	53-55	20-21	33-34	0	15,22,22-24	2	24,26,22-23	57-58	-	-	-	-
Merluccius albidus	165-185	4	51-52	25	26-27	0	12,13,36-37	0	37-38	39-42	-	-	-	-
Merluccius bilinearis	245-300	4	54	27-28	26-27	0	12,13,39-41	0	38-41	34-36	-	-	-	-
Phycis chesteri	198-266	4	47-49	15	32-34	0	10,55-60	0	48-54	20-31	-	-	-	-
Urophycis chuss	80-105	4	48	15	33	0	9-10,53-58	0	45-54	30	-	-	-	-
Urophycis cirratus	317-337	3	51	16	35	0	10,62-64	0	54-55	32	-	-	-	-
Urophycis earlli	282	1	46	15	31	0	10,59	0	53	30	-	-	-	-
Urophycis regius	82-177	4	45-46	13-14	31-33	0	8-9,47-51	0	45-50	30-32	-	-	-	-
Urophycis tenius	84-135	4	56-57	14-15	42	0	6,57-59	0	53-57	-	-	-	-	-
GEMPYLIDAE														
Gempylus serpens	210	1	53	34	19	32	12+8	3	-	29	4	9	8	8
Lepidocybium flavobrunneum	373	1	32	17	15	9	19+5	3	12+4	37	10	9	8	10
Neopinnula orientalis	115-167	4	32	16	16	17	18	3	18	35-37	9-10	9	8	9-10
Nesiarchus nasutus	215-245	3	36	22	14	22-23	22-23	3	18-19	33-34	7-8	9	8	9
Ruvettus pretiosus	270-310	3	32	16	16	13-15	18-19+2	2	17-18+2	34-37	9-10	9	8	8-10
GERRIDAE														
Diapterus olisthostomus	160-163	2	24	10	14	9	10	3	8	38	11	9	8	10
Diapterus rhombeus	90-105	4	24	10	14	9	10	2	9	37-38	10-11	9	8	10
Eucinostomus argenteus	123-145	4	24	10	14	9	10	3	7	37-38	10-11	9	8	10
Eucinostomus gula	107-143	4	24	10	14	9	10	3	7	37-38	10-11	9	8	10
Eucinostomus lefroyi	128	1	24	10	14	9	10	3	8	36	10	9	8	9
Gerres cinereus	180	1	24	10	14	9	10	3	7	33	8	9	8	8
GOBIESOCIDAE														
Gobiesox strumosus	36-49	4	25-26	14	11-12	0	11	0	10	-	-	-	-	-
GOBIIDAE														
Gobionellus boleosoma	35	3	26	10	16	6	11	0	12	32	9	8	7	8
Gobionellus stigmaticus	51	1	26	10	16	6	12	0	13	30	8	8	7	7
Gobiosoma bosci	29-50	4	27	11	16	9	12-13	0	11	30-32	8-9	8	7	8-7
Gobiosoma ginsburgi	28	1	27	11	16	9	12	0	11	32	9	8	7	8
Gobiosoma robustum	25-31	4	27	11	16	7	11-12	0	10-12	31-32	8-9	8	7	7-9
Microgobius gulosus	31-45	4	27	11	16	7-8	16-17	0	17-18	30	8	8	7	7
GRAMMATIDAE														
Argyripnus atlanticus	60-73	4	46-47	16	30-31	8	10-11	0	-	-	-	10	9	-
Bonapartia pedalota	51-70	2	37-38	17	20-21	0	19	0	29	-	-	10	9	-
Gonioma bathyphilum	127	2	38-39	17	21-22	0	13	0	24	-	-	-	-	-
Gonostoma elongatum	135-215	4	41	17	24	0	13-14	0	29-31	38-41	10-12	10	9	9-10
Maurolicus muelleri	43	4	32-33	12	20-21	0	-	0	-	-	-	-	-	-
Polymetme corythaeola	122-165	4	45	18	27	8	11-12	0	28-34	-	-	10	9	-
Triplophos hemingi	172-183	2	59	19	40	8	10-11	0	57	-	-	-	-	-
GRAMMICOLEPIDAE														
Grammicolepis brachiusculus	78-90	4	36-37	10	26-27	6	27-29	2	27-29	17	1	7	8	1
Xenolepidichthys dalgleishi	70-75	4	37-38	10	27-28	8	29	2	28-29	17	1	7	8	1
GRAMMISTIDAE														
Rypticus bistrispinus	61-70	4	25	10	15	2	25-26	2	15-16	24-26	4-5	9	8	3-4
Rypticus maculatus	82-152	4	24	10	14	2	24-25	2	15-16	25-26	4-5	9	8	4
Rypticus saponaceus	50-175	4	24	10	14	3	24-25	2	17	24-25	3-4	9	8	4
HOLOCENTRIDAE														
Corniger spinosus	103-124	4	27	11	16	12-13	13-14	4	11	28-29	5	10	9	4-5
Holocentrus ascensionis	141-200	4	27	11	16	11	15	4	10	30	6	10	9	5
Holocentrus bullisi	74-108	4	27	11	16	11	11-12	4	7-8	30	6	10	9	5
Holocentrus coruscus	105	1	27	11	16	11	11	4	7	30	5	10	9	5
Holocentrus rufus	48-153	8	27	11	16	11	14-15	4	9-10	29-30	6	10	9	4-5
Holocentrus vexillarius	61-65	4	27	11	16	11	13	4	9	30-31	6	10	9	5-6
Myripristis [illegible]	68-115	4	26	11	15	11	13-15	4	12-13	27-28	5	10	9	3-4
Ostichthys trachypomus	74-105	4	26	11	15	10	12-13	4	11	28	5	10	9	4
ISTIOPHORIDAE														
Tetrapturus albidus	62-80	4	23-24	12	11-12	43-47	6-7	16-18	6-8	35-38	10	9	8	8-11
KYPHOSIDAE														
Kyphosus incisor	34-50	4	26	10	16	10-11	13-14	3	13	34	9	9	8	8
Kyphosus sectatrix	33-53	4	26	10	16	11	12	3	11	33	8	9	8	8

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
LABRIDAE														
Bodianus pulchellus	187-215	3	26	11	17	12	10	3	11-12	32-33	9-10	7	7	9
Clepticus parrai	38	1	28	11	17	12	18	3	12	37	12	7	7	11
Decodon puellaris	115-152	4	28	11	17	11	10	3	10	34-35	10-11	7	7	10-11
Halichoeres bathyphilus	120-137	8	25	10	15	9	11	3	12	26	6	7	7	6
Halichoeres bivittatus	123-140	4	25	10	15	9	11	3	12	26-27	6-7	7	7	6
Halichoeres maculipinna	57-83	8	25	10	15	9	11	3	11	26-27	6-7	7	7	6
Halichoeres radiatus	307	1	25	10	15	9	11	3	12	26	6	7	7	6
Hemipteronotus martinicensis	98	1	25	9	16	9	11	3	12	26	6	7	7	6
Hemipteronotus novacula	118-152	4	25	9	16	8-9	12-13	4	12	21-23	4-5	7	7	3-4
Lachnolaimus maximus	112-122	4	30	13	17	14	11	3	10-11	26-28	6-7	7	7	6-7
Tautoga onitis	383	1	35	17	18	17	11	3	8	28	7	8	7	6
Thalassoma bifasciatum	87	1	25	10	15	8	13	3	11	25	6	7	7	5
Thalassoma nitidum	41-55	8	25	10	15	8	12-13	3	10-11	24-26	5-6	7	7	5-6
LOBOTIDAE														
Lobotes surinamensis	19-40	4	24	11	13	12	15-16	3	11	23-25	3-5	9	8	3
LOPHIIDAE														
Lophius americanus	86-98	2	25-26	14	11-12	-	-	0	9-10	-	-	-	-	-
LUTJANIDAE														
Apsilus dentatus	202	1	24	10	14	10	9	3	8	42	13	9	8	12
Ocyurus chrysurus	157-173	4	24	10	14	10	13	3	8-9	34-35	9	9	8	8-9
Rhomboplites aurorubens	123-134	4	24	10	14	12	11	3	7	40-42	12-13	9	8	11-12
Symphysanodon typus	111-123	4	25	10	15	9	10	3	7	40-42	12-13	9	8	11-12
MALACOSTEIDAE														
Malacosteus niger	90	1	47	-	-	0	18	0	21	-	-	-	-	-
MICRODESMIDAE														
Microdesmus carri	31-34	2	67-68	37	30-31	0	-	0	-	23	5	7	6	5
MORIDAE														
Brosmiculus imberbis	135-165	4	50-53	17	33-34	0	10,53-56	0	56-62	34-37	-	-	-	-
Laemonema barbatulum	90-185	2	59	17	42	0	5-6,59	0	67	28	-	-	-	-
Physiculus fulvus	115-122	4	48-49	14	34-35	0	10-11,50-58	0	60-64	23-24	-	-	-	-
MUGILIDAE														
Agonostomus monticola	28-30	3	25	12	13	5	8	3	10	32-34	9-10	7	7	9-10
Mugil cephalus	105-155	4	24	12	12	5	8	3	8	28-30	7-8	7	7	7-8
Mugil curema	84-105	4	24	12	12	5	8	3	9	28-29	7-8	7	7	7-8
Mugil incilis	35	2	24	12	12	5	8	3	8	29-30	8	7	7	7-8
Mugil trichodon	58-105	4	24	12	12	5	7-8	3	8-9	28-29	7	7	7	7-8
MULLIDAE														
Mulloidichthys martinicus	90-134	4	24	10	14	9	8	2	6	31	8	8	7	8
Mullus auratus	97-126	3	24	10	14	9	8	2	6	33	9	8	7	9
Pseudupeneus maculatus	113-155	4	24	10	14	9	8	2	6	34-35	10	8	7	9-10
Upeneus parvus	100-134	4	24	10	14	8	8	2	6	31	8	8	7	8
MYCTOPHIDAE														
Centrobranchus nigroocellatus	24-27	4	36	16	20	0	9-11	0	16-18	30-31	6	10	9	5-6
Diaphus anteorbitalis	117-162	4	35	16	19	0	15	0	15	31-32	6-7	10	9	6
Diaphus dumerilii	51-80	4	35-36	16	19-20	0	13-14	0	14-15	30-31	6	10	9	5-6
Diaphus lucidus	68-97	5	34	16	18	0	15	0	14	31-32	6-7	10	9	6
Diaphus rafinesquei	68-81	5	34	16	18	0	12-13	0	14	31-32	6-7	10	9	6-7
Diaphus termophilus	48-51	4	35	16	19	0	13-14	0	14-15	32-33	7	10	9	6-7
Lonchthys coccoi	20-47	4	39-40	15	24-25	0	11	0	21-23	31-32	6	10	9	6-7
Myctophum macrochir	33	1	35	16	19	0	12	0	20	34	8	10	9	7
Lepidophanes guentheri	44	1	37	16	21	0	14	0	14	34	8	10	9	7
Lepidophanes suprolateralis	100	1	34	16	18	0	12	0	14	32	7	10	9	6
Myctophum affine	68-76	3	35-37	15	20-22	0	13	0	18-20	34-36	8-9	10	9	7-8
Myctophum aurolaternatum	28-68	4	37	15	22	0	12-13	0	17-18	35-37	8-9	10	9	8-9
Myctophum nitidulum	55-68	4	38	15	23	0	13	0	19-20	35-37	8-9	10	9	8-9
Myctophum obtusirostris	42-61	2	35	15	20	0	13	0	18	34-35	8	10	9	7-8
Notoscopelus elongatus	25	1	38	17	21	0	21	0	-	44	12	10	9	13
Symbolophorus rufinus	51-52	2	37	15	22	0	14-15	0	20-21	36-37	9	10	9	8-9
NEOSCOPELIDAE														
Neoscopelus macrolepidotus	117-136	4	31-32	14	17-18	0	13	0	12-13	34	8	10	9	7
OGCOCEPHALIDAE														
Dibranchus atlanticus	75-142	3	18	5	13	-	-	-	-	-	-	-	-	-
Halieutichthys aculeatus	65-87	4	17	5	12	-	-	-	-	-	-	-	-	-
Ogcocephalus cubifrons	110-127	4	19	-	-	-	-	-	-	-	-	-	-	-
Ogcocephalus parvus	55-95	4	18	-	-	-	-	-	-	-	-	-	-	-
Ogcocephalus vespertilio	100-130	4	17-18	-	-	-	-	-	-	-	-	-	-	-
OPHIDIIDAE														
Lepophidium brevibarbe	165-260	4	72	15	57	0	127-129	0	106-111	-	0	-	-	8
Lepophidium cervinum	190-240	4	72-74	15	57-59	0	132-134	0	112-117	9	0	4	5	0
Lepophidium jeannae	210-275	4	74-75	14	59-61	0	135-139	0	114-116	8	0	4	4	0
Lepophidium kallion	155-165	2	71-72	14	52-58	0	130-135	0	108-115	9	0	4	5	0
Lepophidium microcephalum	150-180	8	71-72	14-15	57	0	128	0	108	9	0	4	5	0
Lepophidium profundorum	200-220	4	72	14	57	0	126-132	0	106-108	9	0	4	5	0
Ophidion beani	210-230	4	66-67	16	50-51	0	135-125	0	96-100	8	0	4	4	0
Ophidion grayi	190-265	4	64-65	16	48-49	0	133-144	0	98-105	9	0	4	5	0
Ophidion holbrooki	125-260	4	66-67	16	50-51	0	120-136	0	98-111	9	0	4	5	0
Ophidion welshi	175-210	4	66-67	16	50-51	0	138-146	0	116-121	9	0	4	5	0
Otophidium omostigmum	60-122	3	57-59	14	43-45	0	102-105	0	82-85	8	0	4	4	0
Rissola marginata	145-180	4	68-69	15	53-54	0	147-158	0	118-124	9	0	4	5	0

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
SCIAENIDAE														
Bairdiella chrysura	40-142	12	25	11	14	12	19-22	2	8-10	31-34	8-9	9	8	5-8
Bairdiella ronchus	135-153	2	25	11	14	11	23-24	2	8	34	9	9	8	8
Cynoscion arenarius	150-177	3	25	13	12	11	25-27	2	10-12	28-33	6-8	9	8	5-8
Cynoscion floridanus	180-215	4	25	13	12	11	24-26	2	9	30-32	7-8	9	8	6-7
Cynoscion leiarchus	112-178	3	25	13	12	11	21-23	2	11	31-32	7-8	9	8	7
Cynoscion nebulosus	31-220	8	25	13	12	11-12	24-27	2	10-11	29-33	6-9	9	8	5-7
Cynoscion nothus	121-130	4	27	14	13	11	28-30	2	9	30-32	7-8	9	8	6-8
Cynoscion regalis	28-165	10	25	13	12	11	24-28	2	10-12	29-33	7-9	9	8	5-7
Cynoscion virescens	90-175	5	25	14	11	11	27-30	2	7-8	26-31	6-7	9	8	5-7
Equetus acuminatus	90-104	6	25	10	15	10-11	36-40	2	6-8	30-32	7-8	9	8	6-7
Equetus lanceolatus	100-122	4	25	10	15	13-14	46-50	2	6	27-28	6-7	9	8	4-5
Equetus punctatus	77-197	5	25	10	15	13	44-49	2	7-8	29-31	7	9	8	5-7
Equetus umbrosus	148-165	4	25	10	15	9-11	38-39	2	7	31-32	7-8	9	8	7
Isopisthus parvipinnis	112-173	4	25	10	15	7	20	2	19-20	30-35	7-9	9	8	6-9
Larimus breviceps	152-173	4	25	10	15	11	24-28	2	6-7	29-30	6-7	9	8	6
Larimus fasciatus	27-130	10	25	10	15	11-12	25-27	2	6	28-31	6-7	9	8	4-7
Leiostomus xanthurus	27-182	15	25	10	15	11-12	29-32	2	12-13	29-33	6-8	9	8	6-8
Macrodon ancylodon	221-230	3	26	14	12	10-11	29-30	2	9-10	30	6-7	9	8	6-7
Menticirrhus americanus	172-195	4	25	10	15	11	24-26	2	7-8	32-33	8-9	9	8	7
Menticirrhus littoralis	72-143	4	25	10	15	11	24-25	2	7	30-31	7-8	9	8	6
Menticirrhus martinicensis	210-233	2	25	10	15	11	23	2	7	31-32	8	9	8	6-7
Menticirrhus saxatilis	75-213	4	25	10	15	11	23-25	2	7-8	29-31	6-8	9	8	6
Micropogon furnieri	140-235	5	25	10	15	11	26-28	2	7-8	34-36	9-10	9	8	7-9
Micropogon undulatus	101-200	5	25	10	15	11	26-29	2	8	33-34	8-9	9	8	8
Nebris microps	148-177	4	25	11	14	9	30-34	2	10	31-33	8	9	8	6-8
Odontoscion dentex	115-180	4	25	12	13	12	21-23	2	9	35-37	9-11	9	8	9
Ophioscion costaricensis	118	1	25	10	15	11	21	2	9	35	9	9	8	9
Paralonchurus brasiliensis	132-153	4	29	11	18	11	29-30	2	8	28-30	6	9	8	5-7
Paralonchurus peters	105-155	4	25	10	15	11	31-33	2	7	27-28	5	9	8	5-6
Pogonias cromis	28-163	6	24	10	14	11	21-23	2	6	32-33	8-9	9	8	7
Sciaenops ocellata	20-26	5	25	10	15	11	23-25	2	7-8	32-36	8-10	9	8	7-9
Stellifer lanceolatus	38-108	7	25	10	15	12-13	21-24	2	7-9	30-35	7-9	9	8	6-9
Stellifer rastrifer	137-168	4	25	10	15	12-13	21-23	2	8-9	33-36	7-10	9	8	7-9
Stellifer stellifer	47	1	24	9	15	12	20	2	8	34	9	9	8	7
Umbrina gracilicirrhus	87-174	4	25	10	15	11	22-23	2	7-8	30-33	7-8	9	8	6-
SCOMBERESOCIDAE														
Scomberesox saurus	51-58	5	66-67	40	26-27	0	10-11+5	0	13+6	21-25	3-4	7	8	3-6
SCOMBRIDAE														
Auxis thazard	52-115	5	39	20	19	11-12	11-12+8	-	14+7-8	41	13	9	8	11
Euthynnus alletteratus	38	1	39	19	20	17	12+7	-	13+7	-	-	9	8	-
Euthynnus pelamis	370	1	41	22	19	16	14+9	2	13+7	-	-	9	8	-
Sarda sarda	330	1	50	25	25	22	14+9	3	11+7	-	-	9	8	-
Scomber japonicus	170-180	4	30-31	14	16-17	10-11	12-14+5	2	13+5	35-38	8-11	9	8	10
Scomber scombrus	68	1	31	14	17	11	11+5	2	13+5	-	-	9	8	-
Scomberomorus cavalla	120-250	5	42-43	17	25-26	16	14-16+8-11	4	13-15+8-9	43-44	13-14	9	8	13
Scomberomorus maculatus	155-220	4	52-53	21	31-32	18-19	18-19+8-9	4	14-16+7-8	41	12	9	8	12
Thunnus albacares	580	1	39	18	21	13	12+-	-	12+-	-	-	9	8	-
Thunnus atlanticus	500	1	39	19	20	14	14+8	1	12+7	-	-	9	8	-
Thunnus thynnus	75	1	39	18	21	17	12+8	2	12+7	45	15	9	8	13
SCORPAENIDAE														
Helicolenus dactylopterus	186-210	4	25	10	15	12	12	3	5	34-36	10-12	7	7	9-10
Neomerinthe beanorum	75-91	4	24	9	15	12	9	3	5	26-29	7-8	7	7	5-7
Neomerinthe pollux	222	1	24	9	15	12	10	3	5	27	7	7	7	6
Pontinus castor	61-69	3	24	9	15	12	10-11	3	5	25-27	6-7	7	7	5-6
Pontinus longispinis	108-135	4	24	9	15	12	9	3	5	27-28	7	7	7	6-7
Pontinus macrolepis	54-76	4	24	9	15	12	9	3	5	27-29	7-8	7	7	6-7
Pontinus rathbuni	83-105	3	24	9	15	12	9	3	5	27	7	7	7	6
Scorpaena agassizi	86-127	4	24	9	15	12	9	3	5	25-26	6	7	7	5-6
Scorpaena bergi	71-133	3	24	9	15	12	9	3	5	27-29	7-8	7	7	6-7
Scorpaena brasiliensis	92-187	4	24	9	15	12	8-10	3	5	26-28	6-7	7	7	6-
Scorpaena calcarata	107-135	4	24	9	15	12	9	3	5	25-27	6-7	7	7	5-6
Scorpaena dispar	96-126	4	24	9	15	12	9	3	5	26-27	6-7	7	7	6
Scorpaena inermis	72-158	3	24	9	15	12	8-9	3	5	26	6-7	7	7	5-6
Scorpaena isthmensis	91-122	4	24-25	9	15-16	12	9	3	5	27-29	7-8	7	7	6-7
Scorpaena petricola	24	1	24	9	15	12	9	3	5	25	7	7	7	5
Scorpaena plumieri	165-197	2	24	9	15	12	9	3	5-6	24-25	5-6	7	7	5
Setarches guentheri	85-130	4	24	10	14	12	9	3	5	29	8	7	7	7
Trachyscorpia cristulata	147-204	3	25	9	16	12	9	3	5	30	8	7	7	8

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
OPISTHOGNATHIDAE														
Lonchopisthus higmani	54–84	4	28	10	18	11	18	3	16–17	23	3–4	8	8	3–4
Opisthognathus macrognathus	116–131	2	30	10	20	11	17	3	17	23	4	8	8	3
Opisthognathus maxillosus	75–105	3	28	10	18	11	15	3	14–15	24–25	5	8	8	3–4
OSTRACIIDAE														
Lactophrys polygonia	26–120	4	13	8	5	0	10	0	-	-	0	5	5	0
Lactophrys quadricornis	42–148	5	14	8	6	0	10	0	-	-	0	5	5	0
PEMPHERIDAE														
Pemphris schomburgki	82	1	25	10	15	5	8	3	32	29	7	9	8	5
PERCOPHIDIDAE														
Bembrops anatirostris	130–216	4	28	9	19	6	14–15	0	17–19	34–36	10–11	8	7	9–10
Bembrops gobioides	163–192	4	30	9	21	6	16–17	0	17–18	34–36	10–11	8	7	9–10
Bembrops macroma	145–160	4	28	9	19	6	14	0	17–18	36–37	11–12	8	7	10
Chirosyrtes squamentum	72–74	2	28	9	19	6	15	0	18	40–41	13	8	7	12–13
PLEURONECTIDAE														
Glyptocephalus cynoglossus	220–230	2	57–58	11–12	45–47	0	108–117	0	91–101	22–23	0–1	11	11	0
Pseudopleuronectes americanus	104–107	4	40–41	10	30–31	0	61–64	0	53–54	20	1	9	8	2
Pseudopleuronectes herzensteini	90–104	4	41–42	10	31–32	0	63–66	0	53–56	20	1	9	8	2
POECILIIDAE														
Gambusia affinis	23–26	4	32–33	14	18–19	0	7–8	0	11	23–26	-	-	-	-
Heterandria formosa	16–20	4	31	14	17	0	7–8	0	9	24	-	-	-	-
Poecilia latipinna	20–24	4	29–30	13–14	15–17	0	13–14	0	8	30–32	-	-	-	-
POLYMIXIIDAE														
Polymixia lowei	108–127	4	28	12	16	5	29–30	4	15	29	6	9	9	5
Polymixia nobilis	130–195	3	28	12	16	5	35–36	4	16–17	29	6	9	9	5
POLYNEMIDAE														
Polydactylus octonemus	63–66	4	24	10	14	9	11–12	3	13	41–43	12–13	9	8	12–13
Polydactylus virginicus	22–24	3	24	10	14	8–9	10–12	3	12–13	-	-	9	8	-
POMACENTRIDAE														
Abudefduf analogus	115	1	26	11	15	13	12	2	10	26	6	8	7	5
Abudefduf saxatilis	55–126	3	26	11	15	13	13	2	12	26–27	6	8	7	5–6
Chromis enchrysurus	75–82	4	26	11	15	13	12	2	12	25	5	8	7	5
Chromis insolatus	55–60	4	26	11	15	13	12	2	11	24–25	5	8	7	4–5
Pomacentrus fuscus	55–62	4	26	11	15	12	15–16	2	13–14	25	5	8	7	5
Pomacentrus leucostictus	40–51	4	26	11	15	12–13	15	2	13	25	5	8	7	5
Pomacentrus planifrons	38	1	26	11	15	12	15	2	13	25	5	8	7	5
POMADASYIDAE														
Anisotremus surinamensis	119–165	2	26	10	16	11–12	17–18	3	9	42–43	13	9	8	12–13
Anisotremus virginicus	86–178	3	26–27	10	16–17	12	16–17	3	10–11	38–39	10–11	9	8	10–11
Conodon nobilis	135–155	4	26	10	16	12	13	3	8	39–40	11–12	9	8	11
Genyatremus luteus	148–190	4	26	10	16	13	11–13	3	11	35–37	10	9	8	8–10
Haemulon album	161–238	2	26	10	16	12	16–17	3	7–8	39–40	12–13	9	8	9–11
Haemulon aurolineatum	93–133	4	26	10	16	13–14	14–15	3	9	38–41	11–12	9	8	10–11
Haemulon chrysargyreum	128	1	26	10	16	12	14	3	9	41	13	9	8	11
Haemulon flavolineatum	95–135	3	26	10	16	12	14	3	8	33–36	9–10	9	8	8–9
Haemulon melanurum	97–135	4	26	10	16	12	15–16	3	8	37–40	10–12	9	8	10–11
Haemulon plumieri	77–227	4	26	10	16	12	15–16	3	9	37–39	9–12	9	8	10–11
Haemulon steindachneri	137–160	4	26	10	16	12	16	3	9	39–41	11–12	9	8	11–12
Haemulon striatum	88–102	4	26–27	10	16–17	13	13–15	3	8–9	39–42	12–13	9	8	10–12
Orthopristis chalceus	117–163	4	26	10	16	12–13	15	3	10–11	41	12–13	9	8	11–12
Orthopristis chrysopterus	95–103	4	26	10	16	12–13	15–16	3	13	40–42	12–13	9	8	11–12
Orthopristis ruber	152–185	4	26	10	16	12	15	3	10	38–40	12	9	8	9–11
Pomadasys corvinaeformis	125–170	4	26	10	16	12	15–16	3	7	38–39	11–12	9	8	10–12
POMATOMIDAE														
Pomatomus saltatrix	142–210	4	25	11	15	9	24–25	3	26–28	35–36	9–10	9	8	9–10
PRIACANTHIDAE														
Cookeolus boops	158	1	23	10	13	10	12	3	12	25	5	8	8	4
Priacanthus arenatus	137–188	4	23	10	13	10	14	3	14–15	26–28	5–6	8	8	5–6
Priacanthus cruentatus	135	1	23	10	13	10	13	3	14	24	4	8	8	4
Pristigenys alta	89–135	4	23	10	13	10	11	3	10	24	4	8	8	4
RACHYCENTRIDAE														
Rachycentron canadum	455	1	25	11	14	10	29	2	24	41	16	9	8	8
SCARIDAE														
Cryptotomus roseus	57–67	3	25	10	15	9	10	3	9	25–27	7	7	6	5–6
Nicholsina usta	117–148	3	25	10	15	9	10	3	9	26–28	7–8	7	6	6–7
Scarus croicensis	69–210	3	25	10	15	9	10	3	9	25–27	6–7	7	6	6–7
Sparisoma chrysopterum	67–95	3	25	10	15	9	10	3	9	28	8	7	6	7
Sparisoma radians	81–121	4	25	10	15	9	10	3	9	25–27	6–7	7	6	6–7
Sparisoma rubripinne	74–92	2	25	10	15	9	10	3	8–9	26–28	7–8	7	6	6–7
Sparisoma viride	192	1	25	10	15	9	10	3	9	28	8	7	6	7

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

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			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.	Number											
SYNANCEIDAE														
Anthiasicus leptus	191-295	4	26	10	16	10	14	3	8	40-43	13-14	8	7	12-14
Centropristis ocyurus	124-155	4	24	10	14	10	11	3	7	34-35	9-10	9	8	8
Centropristis philadelphica	101-167	4	24	10	14	10	11	3	7	34-35	9-10	9	8	7-9
Centropristis striata	97-180	4	24	10	14	10	11	3	7	34-35	9-10	9	8	8
Cephalopholis fulva	78-235	4	24	10	14	9	15	3	8-9	35-36	9-10	9	8	9
Chorinitium cubrines	82	1	24	10	14	8	12	3	8	33	8	9	8	8
Hemanthias vivanus	373	1	24	10	14	11	13	3	9	31	7	9	8	7
Diplectrum bivittatum	105-113	4	24	10	14	10	17	3	7	39-40	12	9	8	10-11
Diplectrum formosum	133-175	4	24	10	14	9-10	12	3	7	38-40	11-12	9	8	10-11
Diplectrum radiale	92-155	4	24	10	14	10	12	3	7	37	11-12	9	8	8-9
Epinephelus drummondhayi	275-285	2	24	10	14	11	16	3	9	37-40	10-12	9	8	10-11
Epinephelus flavolimbatus	165-205	4	24	10	14	11	14	3	9	33-35	8-9	9	8	8-9
Epinephelus gutiatus	177-205	2	24	10	14	11	16	3	8	35-37	9-10	9	8	9-10
Epinephelus mystacinus	148	1	24	10	14	11	14	3	9	34	9	9	8	8
Epinephelus nigritis	170	1	24	10	14	10	14	3	9	33	8	9	8	8
Epinephelus niveatus	74-146	4	24	10	14	11	13-14	3	9	33-34	8-9	9	8	7-8
Epinephelus striatus	100-202	2	24	10	14	11	17	3	8	36	10	9	8	9
Hemanthias vivanus	52-102	6	26	10	16	9-10	13-14	3	8	39-41	12-13	8	7	11-13
Hyporthodus nigritus	120	1	24	10	14	11	17	3	12	38	11	9	8	10
Hyporthodus niveatus	240	1	24	10	14	11	17	3	11	38	11	9	8	10
Hyporthodus striatus	127	1	24	10	14	11	16	3	11	37	10	9	8	10
Hyporthodus flavolimbatus	122-205	3	24	10	14	11	16-17	3	10-12	37	10-11	9	8	9-10
Hyporthodus mystacinus	49-66	3	24	10	14	11	16-17	3	11	37-38	10-11	9	8	9-10
Hyporthodus nigritus	393	1	24	10	14	11	16	3	11	37	10	9	8	10
Hyporthodus niveatus	74-104	4	26	10	16	10	15	3	7	33	9	8	7	9
Paranthias furcifer	66-94	2	24	10	14	9	18-19	3	9	40	12	9	8	11
Petroscirtes ecri	103-125	3	24	10	14	9	14	3	8	33-34	8-9	9	8	8
Pikea cubensis	66-107	4	24	10	14	8	13	3	7-8	34-35	9	9	8	8-9
Pronotogrammus aureorubens	125-195	4	26	10	16	10	15	3	8	33-34	9-10	8	7	9
Schultzea beta	52-57	4	24	10	14	10	11-12	3	7	36-38	10-11	9	8	9-10
Serraniculus pumilio	21-44	3	24	10	14	9-10	11	3	7	34-35	9-10	9	8	7-8
Serranus annularis	45-66	4	24	10	14	10	12	3	7	32-33	8	9	8	7-8
Serranus atrobranchus	75-87	4	24	10	14	10	11-12	3	7	35-36	10	9	8	8-9
Serranus chionaraia	33-47	4	24	10	14	10	11-12	3	7	32	8	9	8	7
Serranus baytai	59-72	4	24	10	14	10	11-12	3	6-7	37-38	10-11	9	8	10
Serranus notospilus	99-125	4	24	10	14	10	12	3	7	38-39	11-12	9	8	10-11
Serranus phoebe	112-140	4	24	10	14	10	12	3	7	36-38	10-11	9	8	9-10
Serranus subligarius	60-76	4	24	10	14	10	13-14	3	7	33-39	7-8	9	8	7
Serranus tabacarius	48-117	4	24	10	14	10	12	3	7	34-36	9-10	9	8	8-9
Serranus tortugarum	49-63	3	24	10	14	10	12	3	7	33-34	8-9	9	8	8
SOLEIDAE														
Achirus inscriptus	70-93	5	27-28	9	18-19	0	54-58	0	40-44	15-16	0	7-8	8	0
Achirus lineatus	94-118	3	28	9	19	0	53-58	0	40-43	16	0	8	8	0
Gymnachirus melas	52-117	6	35-36	9	26-27	0	60-70	0	44-51	16	0	8	8	0
Trinectes maculatus	60-92	4	28-29	9	19-20	0	51-55	0	41-42	16	0	8	8	0
SPARIDAE														
Archosargus probatocephalus	69-112	4	24	10	14	12	10-12	3	9-10	32-33	8-9	9	8	7
Archosargus rhomboidalis	168-225	3	24	10	14	13	10-11	3	10	32-33	8	9	8	7-8
Diplodus holbrooki	137-157	4	24-25	10-11	14	12-13	14-15	3	13-14	33-34	8-9	9	8	8
Lagodon rhomboides	72-76	4	24	10	14	12	11	3	11	34-38	10-11	9	8	7-10
Pagrus sedecim	129-162	4	24	10	14	18	10	3	8	35-37	9-10	9	8	9-10
Stenotomus caprinus	109-148	4	24	10	14	12	12	3	11-12	33-34	9	9	8	7-8
Stenotomus chrysops	107-144	4	24	10	14	12	12	3	11	34-37	9-10	9	8	8-10
SPHYRAENIDAE														
Sphyraena borealis	122-206	2	24	12	12	6	9	2	9	35	9	9	8	9
Sphyraena guachancho	168-220	4	24	12	12	6	9	2	8	36	10	9	8	9
Sphyraena picudilla	254	1	24	12	12	6	9	2	9	35	9	9	8	9
STEPHANOBERYCIDAE														
Stephanoberyx monae	70	2	30-31	10	20-21	0	12-13	0	11-12	39-41	10-11	10	9	10-11
STERNOPTYCHIDAE														
Argyropelecus aculeatus	50-57	4	35-36	11	24-25	0	9	0	7+7	32-36	8-11	10	9	5-6
Argyropelecus affinis	51-57	4	35-39	11	27-28	0	7-9	0	7+5	-	9-10	10	9	-
Argyropelecus gigas	52	1	39	11	28	0	9	0	7+5	-	9	10	9	-
Argyropelecus hemigymnus	19-21	2	38	11	27	0	-	0	-	-	-	-	-	-
Polyipnus asterioides	50-67	4	33	10	23	0	14-15	0	15-17	35-36	9-11	10	9	6-7
Polyipnus laternatus	27-40	4	33-34	10	23-24	0	14-15	0	15-16	36	10	10	9	7
Sternoptyx diaphana	32-47	5	29-30	11	18-19	0	9-11	0	14	33-35	7-8	10	9	7-8
STROMATEIDAE														
Cubiceps melanus	128-164	4	30-31	15-16	15	12	15-16	3	14-15	35-37	9-10	9	8	9-10
Cubiceps pleriargenteus	100-115	4	31	15	16	12	15	3	15	35-37	9-10	9	8	9-10
Nomeus gronovii	86-138	4	41-42	16	25-26	12-13	27-28	2	26-27	34-35	8-9	9	8	9
Peprilus alepidotus	61-77	4	30	13	17	3	41-46	3	41-43	28	6	9	8	5
Peprilus paru	178	1	30	13	17	3	43	3	40	29	6	9	8	6
Poronotus triacanthus	115-120	4	32	12	20	3	43-47	3	39-44	31-44	7-9	9	8	7-8
Psenes cyanophrys	67-123	4	31	14	17	11	25-26	3	26-27	33-34	8-9	9	8	8
Psenes pacificus	75-112	3	31	14	17	10-11	25-28	3	24-25	32-34	8-9	9	8	7-8
Psenes regulus	83-193	4	31	14	17	12-13	14-15	3	14-15	36-41	10-12	9	8	9-12
Tetragonurus atlanticus	160	1	45	23	22	15	9	2	9	36	11	8	7	10
STYLEPHORIDAE														
Stylephorus chordatus	215	1	53	-	-	-	-	-	-	-	-	-	-	-
SYNGNATHIDAE														
Hippocampus erectus	105-180	4	49-51	13	36-38	0	19-20	0	-	0	0	0	0	0
Micrognathus crinigerus	65	1	56	17	39	0	-	0	-	-	-	-	-	-
Syngnathus dunckeri	47-52	4	50-53	18	32-35	0	-	0	-	10	-	-	-	-
Syngnathus elucens	40	2	49-50	18	31-32	8	-	0	-	10	-	-	-	-
Syngnathus floridae	115-122	3	51-52	18	33-34	0	-	0	-	-	-	-	-	-
Syngnathus fuscus	108-295	4	55-60	19-21	36-39	0	35	0	-	10	-	-	-	-
Syngnathus louisianae	175-240	4	51-52	19-20	32	0	-	0	-	10	-	-	-	-
Syngnathus mackayi	185-240	4	50-53	20	30-33	0	27-28	0	-	10	-	-	-	-
Syngnathus pelagicus	72-102	4	49-52	18-19	31-33	0	28-29	0	-	10	-	-	-	-
Syngnathus scovelli	87-95	4	49-51	17-18	31-33	0	29-32	0	-	-	-	-	-	-
Syngnathus springeri	55-263	7	61-62	24-25	37-38	0	-	0	-	10	-	-	-	-

TABLE 1.—Meristic characters of some marine fishes of the western North Atlantic Ocean.—Continued.

FAMILY Genus, species	Size range SL	Specimens examined	VERTEBRAE			DORSAL FIN		ANAL FIN		CAUDAL FIN				
			Total	Precaudal	Caudal	Spines	Rays	Spines	Rays	Total	Dorsal secondary rays	Dorsal primary rays	Ventral primary rays	Ventral secondary rays
	mm	No.					Number							
SYNODONTIDAE														
Saurida brasiliensis	50-112	5	46-50	-	-	0	11	0	11	37-40	9-11	10	9	9-10
Saurida caribbaea	80-108	5	52-58	-	-	0	11-12	0	11-12	40-42	11-12	10	9	10-11
Saurida normani	53-330	6	49-52	-	-	0	11-12	0	10-11	41-45	11-13	10	9	11-13
Saurida suspicio	32-72	5	49-52	-	-	0	10-11	0	10-11	38-40	10-11	10	9	9-10
Synodus foetens	89-345	5	56-61	-	-	0	11-12	0	12	41-43	11-12	10	9	11-12
Synodus intermedius	62-190	5	47-50	-	-	0	12-13	0	11-12	40-42	11-12	10	9	10-11
Synodus poeyi	60-165	8	44-46	-	-	0	10-11	0	10	39-44	10-13	10	9	10-12
Synodus saurus	32-213	6	55-58	-	-	0	12-13	0	9-11	46-49	14-16	10	9	13-14
Synodus synodus	35-149	6	54-57	-	-	0	12-13	0	8-9	43-49	12-16	10	9	12-14
Trachinocephalus myops	84-207	5	54-57	-	-	0	11-13	0	14-15	45	13	10	9	13
TETRAODONTIDAE														
Canthigaster rostrata	58	1	17	8	9	0	9	0	8	11	0	5	6	0
Lagocephalus laevigatus	74-152	4	19	8	11	0	14-15	0	12-13	11	0	5	6	0
Sphoeroides dorsalis	107-113	3	18	8	10	0	9	0	8	11	0	5	6	0
Sphoeroides dorsalis	118-187	4	17	8	9	0	8	0	7	11	0	5	6	0
Sphoeroides maculatus	99-178	3	19	8	11	0	8	0	7	11	0	5	6	0
Sphoeroides nephelus	50-142	5	19-20	8	11-12	0	8	0	7	11	0	5	6	0
Sphoeroides spengleri	100-125	4	17-18	8	9-10	0	8	0	8	11	0	5	6	0
Sphoeroides testudineus	72-129	4	18	8	10	0	8	0	7	11	0	5	6	0
TRACHICHTHYIDAE														
Hoplostethus mediterraneus	75-88	4	26	11	15	6	13	3	9	33-34	7-8	10	9	7
TRIACANTHODIDAE														
Hollardia hollardia	71-90	4	20	8	12	6	16-17	0	18	12	0	6	6	0
Parahollardia schmidti	51-60	4	20	8	12	6	35	0	13	12	0	6	6	0
TRICHIURIDAE														
Benthodesmus simonyi	590	1	157	-	-	-	-	2	-	-	-	-	-	-
Benthodesmus tenuis	430-465	4	127-132	-	-	-	121-132	2	71-81	-	-	-	-	-
Trichiurus lepturus	310-380	4	169-173	39-40	130-134	3	132-138	2	89-107	-	-	-	-	-
TRIOLIDAE														
Bellator brachychir	55-63	4	26	10	16	11	10-11	0	11	31-33	9-10	7	6	8-10
Bellator egretta	94-108	4	26	10	16	11	11	0	11	30-32	9-10	7	6	8-9
Bellator militaris	61-92	5	25-26	10	15-16	11	11	0	9-10	27-30	7-9	7	6	7-8
Bellator ribeiroi	30-59	8	26	10	16	11	11	0	9-11	27-28	7-8	7	6	7
Prionotus alatus	81-130	4	26	10	16	10	12-13	0	11	30-31	9-10	7	6	8
Prionotus beani	72-133	4	26	10	16	10	12	0	11	30-31	9	7	6	8-9
Prionotus carolinus	172-188	4	26	10	16	10	13	0	12	31-33	9-10	7	6	9-10
Prionotus evolans	113-157	4	26	10	16	10	12	0	11	32-35	10-11	7	6	9-11
Prionotus horrens	98-137	4	26-27	10	16-17	10	12-13	0	10-11	25-27	6-7	7	6	8-8
Prionotus paralatus	89-118	4	26	10	16	9-10	12	0	11	31-32	9-10	7	6	9
Prionotus pectoralis	157-225	4	26-27	10	16-17	10	12-13	0	11-12	31-34	9-11	7	6	9-11
Prionotus punctatus	97-153	4	26	10	16	10	11-12	0	11	32-35	10-11	7	6	9-11
Prionotus roseus	113-145	4	26	10	16	10	12-13	0	11	29-30	8-9	7	6	8
Prionotus rubio	157-173	4	26	10	16	10	12	0	10-11	31-32	9-10	7	6	9
Prionotus scitulus	79-172	4	26	10	16	10	13	0	12	30-33	10-11	7	6	7-10
Prionotus stearnsi	98-113	4	26	10	16	9-10	12	0	10-11	33-34	10-11	7	6	10
Prionotus tribulus	90-193	4	26	10	16	10	12	0	11	30-33	9-10	7	6	8-10
Peristedion antillarum	92-120	4	31	9	22	6	16	0	-	28	8	6	6	8
Peristedion brevirostre	92-96	2	32	9	23	-	-	0	-	25	7	6	6	6
Peristedion ecuadorensis	127-142	4	33-35	9	24-26	-	-	0	-	25-27	7-8	6	6	6-7
Peristedion gracile	110-130	4	34-35	9	25-26	8	14	0	21-23	27-28	8	6	6	7-8
Peristedion greyae	87-105	3	34-35	9	25-26	8	18-20	0	18-21	28	8	6	6	8
Peristedion imberbe	107-135	4	34-35	9	25-26	8	18	0	-	26-28	7-8	6	6	7-8
Peristedion longispatha	122-135	4	32-33	9	23-24	-	-	0	-	26	7	6	6	7
Peristedion miniatum	118-148	4	33	9	24	-	-	0	-	26-28	7-8	6	6	7-8
Peristedion schmitti	73-94	4	31-33	9	22-24	-	-	0	-	26	7	6	6	7
Peristedion truncatum	115-133	3	33-34	9	24-25	-	-	0	19	26	7	6	6	7
Peristedion unicuspis	136-153	2	33	9	24	8	19-20	0	20	25-26	6-7	6	6	7
URANOSCOPIDAE														
Astroscopus guttatus	230	1	25	11	14	5	13	0	13	22	5	7	6	4
Astroscopus y-graecum	80-110	4	25	11	14	5	13-14	0	13-14	25-26	6-7	7	6	6-7
Gnathagnus egregius	83-125	4	28	11	17	0	12-14	0	16-17	28-29	8-9	7	6	7-8
Kathetosoma albigutta	85-117	3	25	10	15	0	14-15	0	12-13	22	5	7	6	4
Kathetosoma cubana	62-118	5	26	11	15	0	14-15	0	13-14	23	5	7	6	5
XIPHIIDAE														
Xiphias gladius	53-170	4	26	14	12	-	52	-	-	31-32	7-9	9	8	7
ZEIDAE														
Cyttopsis roseus	85-135	4	31	10	21	7	28-29	2	28-29	20-21	3-4	6	7	4
Parazen pacificus	105-118	4	34	12	22	8-9	26-29	1	31-33	27-28	8-9	5	6	8
Zenopsis oscillata	68-75	4	35	12	23	8-9	24-26	3	22-25	15	1	6	7	1
ZENIONTIDAE														
Zenion hololepis	60-72	4	27	11	16	5-6	26-28	1-2	22-23	18	3	6	7	2
ZOARCIDAE														
Macrozoarces americanus	340-390	4	137-138	25-27	111-112	18-21	90-94+28-31	0	113-115	-	-	-	-	-

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FREQUENCY AND DURATION OF FLOW REVERSAL IN THE LOWER COLUMBIA RIVER, APRIL 1968-MARCH 1970

The hydraulic head generated by some heights of tide can result in changes in direction of current in the lower Columbia River when volume discharges fall below a critical value. In connection with this phenomenon, Clark and Snyder (1969) conducted a study to determine the timing and extent of reversal of flow during an extreme condition of low discharge of water from the river. They determined that flow reversals could increase the accumulation of discharged effluents per given volume of river water by as much as 3.5 times over the accumulation at mean flow rates. Their report showed the need for a continuing record of direction of current in the lower Columbia River to determine the importance of flow reversal at different discharge rates. To help satisfy this need, a floating laboratory (Snyder, Blahm, and McConnell, 1971) was established on the lower Columbia River at river kilometer 117.5 (river mile 73) near Prescott, Oreg., where speed and direction of current were recorded. This report describes the flow-reversal phenomenon at river kilometer 117.5 from data collected between April 1968 and March 1970.

Procedure

The velocity of the river current was measured with a Savonius meter[1] suspended from the laboratory to determine the frequency and duration of flow reversal in the lower Columbia River. With the exception of 21 days, the flow was monitored continuously for a 2-year period. Flow data obtained at Prescott were related to the daily discharge of the river and to the time and height of ocean tides near the river's mouth at Astoria, Oreg.

Daily average flow for the period 1 April 1968 to 30 June 1969, was "gauged flow" furnished by the U.S. Geological Survey office in Portland, Oreg.; daily average flow for the period 1 July 1969 to 31 March 1970, was from information furnished by U.S. Geological Survey offices in Portland, Oreg., and Tacoma, Wash. Time and height of oceanic tides were for Astoria, Oreg.; these data were obtained from tide charts of the NOAA (National Oceanic and Atmospheric Administration) National Ocean Survey.

Our observations of direction and speed of current were used to determine the duration and frequency of flow reversals. Only those flow reversals of 60-min duration or longer were considered to constitute true reversals. Duration of flow reversal was defined as the time interval between positive downstream flows wherein the

[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

downstream flow stops, then moves upstream and stops, and then moves downstream again.

Data Analysis

River discharge and height of tide are independent variables in the analysis of flow reversal in the lower Columbia River. The average monthly flow at Prescott is characterized by high bimodal peaks that occur annually in the winter and spring. The higher high tides typically occur during the same period.

River Flow

The flow of the Columbia fluctuated greatly during our study. It averaged 6,768 cubic meters per second (m^3sec^{-1}) or 239,000 cubic feet per second (cfs) and ranged from 2,209 to 14,442 m^3sec^{-1} (78,000 to 510,000 cfs). High flow occurred during June 1968 and May 1969; these high discharges were associated with water from melting snow in areas east of the Cascade Mountains. High river flow in January (Figure 1) was associated with precipitation in areas west of the Cascades. Low flows occurred during September in both years. Average monthly flows exceeded 8,495 m^3sec^{-1} (300,000 cfs) for only 5 months of the 24-month period; this fact is important in that it was only when the flow was below this level that reversal became significant at Prescott.

Tidal Height

High tides ranged from 1.5 to 3.1 m (4.9 to 10.1 ft). Tides of 2.0 to 2.6 m (6.6 to 8.5 ft) occurred most frequently. Tidal influence produces differences in water elevations in the Columbia River that can be measured upstream as far as Bonneville Dam (river km 225.3, river mile 140).

Characteristics of Flow Reversal

During the 2 years of the study, 646 flow reversals of 60 min or longer (Table 1) were observed and related to high tides. Reversals occurred most frequently in August, September, and October—normally the period of lowest discharge—and least frequently in May and June—the period of highest river discharge. Tidal heights at Astoria which produced flow reversals ranged from 1.5 to 3.0 m (4.9 to 9.9 ft).

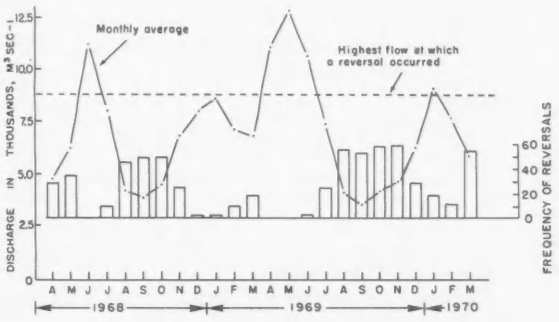

FIGURE 1.—Average monthly Columbia River discharge, at Prescott, Oreg., April 1968-March 1970. Frequency of flow reversals lasting more than 60 min and highest discharge at which a reversal occurred are also indicated.

TABLE 1.—Frequency of flow reversals (≥ 60 min) measured in the lower Columbia River at Prescott, Oreg., April 1968-March 1970.

Period	Number of flow reversals (by month)												Total
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	
1968-69	29	35	0	10	46	49	50	26	3	3	10	19	280
1969-70	0	0	2	25	56	54	57	58	29	19	12	54	366
Total	29	35	2	35	102	103	107	84	32	22	22	73	646

Twenty-one flow reversals of 5 hr or longer were recorded. Few reversals of 60 min or longer were recorded during river discharge above 8,495 m^3sec^{-1} (300,000 cfs), regardless of the height of the tide. This relation is illustrated in Figure 1, where average monthly discharge is compared to the frequency of flow reversal.

The lowest high tide at which reversal was recorded (90 min) was 1.5 m (4.9 ft), at 3,936 m^3sec^{-1} (139,000 cfs). The highest high tide at which a reversal was recorded (155 min) was 3.0 m (9.9 ft) at 6,173 m^3sec^{-1} (218,000 cfs). Two 3-m (10-ft) tides occurred during the study period at 7,759 and 7,985 m^3sec^{-1} (274,000 and 282,000 cfs) without producing a reversal of 60 min or longer. The longest period of reversal was 5¾ hr at a tide height of 2.7 m (8.9 ft) and 5,550 m^3sec^{-1} (196,000 cfs) which occurred 8 March 1970.

A regression analysis was made for each tide level to estimate the critical discharge below which a flow reversal of 60 min or greater could be expected. Discharges that allowed flow reversals at 1.5-, 1.8-, 2.1-, 2.4-, and 2.7-m (5-, 6-, 7-, 8-, and 9-ft) tides were 4,530; 5,720; 5,861; 6,852; and 8,636 m^3sec^{-1} (160,000; 202,000; 207,000; 242,000; and 305,000 cfs; Figure 2). The rate of discharge from the river and tidal height appear to be independent variables while flow reversal is the dependent variable in the analysis.

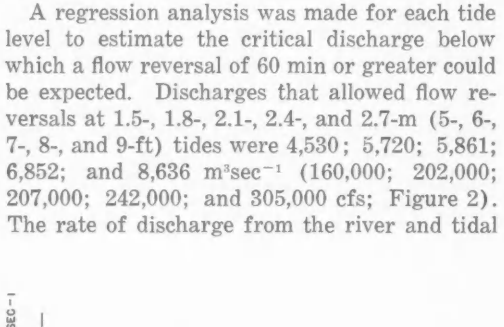

FIGURE 2.—Graphs showing range of flow of the Columbia River for various tidal heights at Astoria, Oreg. The number within each bar is the estimated discharge below which flow reversals of 60 min or longer occur at Prescott, Oreg., for a given tidal height. The number below each bar gives the frequency of occurrence of the tide height for the study period.

Discussion

During the time interval examined, reversal of direction of current ($\geqslant$ 60 min) at Prescott occurred every month except June 1968 and April and May 1969. It is important to discover that the reversals in flow are frequent as previous work in this area only indicated that they could occur at very low river discharges. Because of the frequent occurrence of flow reversals in the region of the lower Columbia River near Prescott, the regulation of waste discharges in this area should receive special attention as these reversals in flow tend to produce pockets of high concentration of wastes in the river system when the waste discharges are constant in time (Clark and Snyder, 1969).

Acknowledgment

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LONG-TERM OLFACTORY "MEMORY" IN COHO SALMON, *ONCORHYNCHUS KISUTCH*[1]

Many experiments have correlated the importance of olfaction and the precise homing of sexually mature salmon. As juveniles, the fish are presumably imprinted on the natural odors of their natal-area water (Hasler, 1966). The odors apparently serve as cues to guide the adult's return. Thus, some type of "odor memory" must persist from the time of the downstream journey of the smolt to the return of the sexually mature adult. For introduced Lake Michigan coho salmon, *Oncorhynchus kisutch*, this is either ½ year (precocious males) or 1½ years.

The existence of long-term olfactory memory persisting over this time period has only been inferred. Idler et al. (1961) and Fagerlund et al. (1963) found that already homed salmon made unconditioned behavioral responses to home water. Hara, Ueda, and Gorbman (1965), Ueda, Hara, and Gorbman (1967), and Oshima, Hahn, and Gorbman (1969a) found specific EEG (electroencephalographic) responses to home-stream water. Hara (1970) in his review of this EEG technique states: "This electric response [from the olfactory bulbs] is specific in the sense that it cannot be evoked by water from spawning sites of other groups of breeding salmon." The EEG and behavioral studies strongly suggest long-term memory of the juvenile's stream experience. However, since these workers used homed adults that had recently experienced home water, the data are evidence only of an odor memory lasting from the time of removal from the home stream to the time of testing.

We tested coho salmon that were exposed to a synthetic odoriferous substance for 1 month during smoltification and then removed from any conceivable influence of this substance for 10 months. Ten months later these fish and controls were examined for olfactory bulbar EEG responses (after Hara et al., 1965) to the imprinting substance.

Materials and Methods

On 7 April 1970, approximately 2,500 hatchery-raised coho salmon smolts (1½ years old) were put into each of two contiguous 25-m sections of a raceway at a Wisconsin State fish hatchery at Crystal Springs. We marked the fish to eventually distinguish the upper section control subjects from the lower section experimentals. A small drop (⅓ m) prevented water in the lower section from reentering the upper section. Immediately below the drop a dilute concentration of morpholine was introduced by infusion pump at a rate to maintain a steady-rate concentration of 10^{-5} ppm. This value is one order of magnitude above an avoidance threshold of unconditioned coho salmon fingerlings (Wisby, 1952). On 5 May 1970, 1 month after initiation of the morpholine treatment, all but 50 fish from each raceway section were trucked to Lake Michigan and released as part of another experiment. The 100 remaining fish were moved to a hatchery near Madison, Wis., and held together in a single outside raceway for 10 months prior to EEG tests.

Our testing procedure was generally similar to that used by Hara et al. (1965) to examine olfactory bulb responses to home-stream water. The subject was paralyzed with gallamine triethiodide (2 mg/kg), restrained, and the gills perfused with tap water. One of the olfactory bulbs was exposed, and an electrode (Transidyne General, model 415[2]) was placed on the surface near the rear margin. The responses evoked by perfusion of the ipsilateral naris were amplified (Bioelectric Instruments, model DS2c) and recorded on a two-channel oscillograph (Hewlett Packard, model 7712B) for later analysis. This oscillograph was equipped with an integrating preamplifier for efficient quantification of bulbar activity. Therefore, all responses reported later

[1] This work was completed under financial support from the National Science Foundation (Grant No. GB 7616X) to Prof. Hasler and the University of Wisconsin Sea Grant Program which is a part of the National Sea Grant Program maintained by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

are expressed as the sum of the positive areas under the response wave form.

Beginning on 25 February 1971, one fish was examined per day with 1% and 0.01% morpholine stimuli. Fourteen fish were used. Each test was started at approximately 1000 hr. Every subject was tested with the morpholine concentrations and the responses compared with responses to 0.06 N NaCl. Stimuli were randomly ordered and presented for 10 sec followed by 75 sec of tap water rinse. The stimulus series was then repeated seven times.

Results

Fish that had been exposed to 10^{-5} ppm of morpholine as smolting juveniles evidenced significantly higher bulbar EEG activity over controls when tested with 1% and 0.01% concentrations of morpholine (Table 1). Responses to 1% morpholine gave a Mann-Whitney value of $U = 5$ (Siegel, 1956) with probability of 0.006 that the control group and the experimental group were drawn from the same treatment population. Responses to the 0.01% level were less markedly, but still significantly, different ($U = 11$, $P = 0.049$).

Discussion

Exposure to low concentrations of morpholine produced a sensitization which lasted at least 10 months. But, we did not attempt to determine whether this observed sensitization was exclusively to morpholine or to other stimulatory products. Casual observation of our data did not reveal the experimental subjects to be more responsive to NaCl than the controls; but this comparison was difficult to make in our experimental design because of the changing relationship between response amplitudes and background activity levels. (Hence, the necessity of continual comparison of morpholine response with NaCl response, our reference.) Even if overall olfactory responsiveness is increased as a result of pretreatment, sensitization to morpholine is still proportionally greater (experimental vs. control) 10 months later. We hypothesize that exposure to morpholine imprinted the fish during one of the critical periods in the life of the coho salmon, a period when the fish is undergoing physiological changes in preparation for entering a marine environment.

Independent evidence indicates the existence of a critical period. The Wisconsin Department of Natural Resources allows approximately 1 month of imprinting during the period of smoltification before releasing the fish into the river system. Imprinting for less time or at different stages of the life cycle seems to result in more straying (Peck, 1970).

Morpholine was chosen as the imprinting substance since the responses of fingerling coho salmon to it have been investigated (Wisby, 1952). Consequently, the concentration could be chosen with knowledge of the performance parameters of the coho salmon. It was necessary to be above threshold but not so high as to cause enthusiastic avoidance or sublethal damage. Because of the vagaries of the flow measurements

TABLE 1.—Morpholine-elicited EEG responses of morpholine-imprinted coho salmon compared with those of controls. E designated subjects were imprinted with morpholine at a concentration of 10^{-5} ppm; C designated were controls. Median EEG responses of each fish to 1% morpholine and 0.01% morpholine stimuli are ranked (ties carry averaged ranks) and Mann-Whitney U values and probability values are shown for each treatment level.

1%														
Group	C	C	C	C	C	C	E	E	E	E	E	C	E	E
Median[1]	63.5	100	140	220.5	230	250	255	266.5	287	333	351.5	600	915	917
Rank	1	2	3	4	5	6	7	8	9	10	11	12	13	14
						$U = 5$	$P = 0.006$							
0.01%														
Group	C	C	E	C	C	C	E	E	C	E	E	C	E	E
Median[1]	0	0	0	0	0	25.6	38.5	41.5	45	45	50	50	67	77.5
Rank	3	3	3	3	3	6	7	8	9.5	9.5	11.5	11.5	13	14
						$U = 11$	$P = 0.049$							

[1] Median response = $\left(\frac{\text{response morpholine}}{\text{response 0.06 N NaCl}} \times 100\right)$ for eight trials.

in the raceway, one order of magnitude above threshold was chosen. Nevertheless, Wisby (1952) reported some avoidance at this concentration. We did not, however, observe any avoidance where the substance was metered into the raceway. It should be noted that concentrations at the delivery tube could be as high as 100 ppm before mixing took place. But, since the substance was delivered immediately below the falls caused by the separating dam, mixing was assumed to be rapid and complete.

Although fish were treated with very low concentrations of the morpholine, EEG responses were not evident until 100 ppm was reached in responsive fish. But, other workers have also found a relative lack of sensitivity with electrophysiological methods. Home-stream responses disappeared with dilution of home-stream water to 5% (Oshima, Hahn, and Gorbman, 1969b), and Sutterlin and Sutterlin (1971), recording from the olfactory epithelium of Atlantic salmon, *Salmo salar*, found no response to morpholine at 0.9 ppm. Yet Wisby (1952) got clear behavioral manifestations of perception at concentrations of 10^{-6} ppm.

Acknowledgments

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HYPORHAMPHUS AUSTRALIS X *HY. MELANOCHIR*, A HYBRID HALFBEAK (HEMIRAMPHIDAE) FROM AUSTRALIA

The purpose of this note is to report the first known occurrence of hybridization in the family Hemiramphidae. According to Schwartz (1972) it is also the first known hybrid within the order Synentognathi (or suborder Exocoetoidei according to some recent classifications).

Three species of sea garfishes (halfbeaks) of the genus *Hyporhamphus* occur in Australia-New Zealand waters (Collette[1]): *Hy. ihi* Phillipps, the New Zealand garfish or piper; *Hy. australis* (Steindachner), the eastern sea garfish; and *Hy. melanochir* (Valenciennes), the southern sea garfish. The three species are very closely related but differ in numbers of gill rakers, vertebrae, dorsal and anal fin rays, relative length of the upper and lower jaw, and placement of the pelvic fins. They are almost completely allopatric but the ranges of *Hy. australis* and *Hy. melanochir* overlap at Eden in southern New South Wales near the Victoria border.

During a year's study at the Australian Mu-

[1] Collette, B. B. The garfishes (Hemiramphidae) of Australia and New Zealand. Unpublished manuscript.

TABLE 1.—Numbers of fin rays, gill rakers, and vertebrae in *Hyporhamphus australis*, *Hy. melanochir*, and a hybrid between the two species.

	Dorsal rays						Anal rays					
	15	16	17	18	*N*	$\bar{x}$	17	18	19	20	*N*	$\bar{x}$
Hy. australis												
New South Wales	29	68	10		107	15.82	12	63	24	2	101	18.16
Eden, N.S.W.		2			2	16		2			2	16
Hybrid-Eden			1		1	17			1		1	19
Hy. melanochir												
Eden			1		1	17			1		1	19
Victoria	1	28	33	2	64	16.56		19	37	8	64	18.83

	First arch gill rakers														
	27	28	29	30	31	32	33	34	35	36	37	38	39	*N*	$\bar{x}$
Hy. australis															
New South Wales					3	6	9	16	23	28	10	6	2	103	35.10
Eden, N.S.W.									1	--	1			2	36
Hybrid-Eden						1								1	32
Hy. melanochir															
Eden			1											1	29
Victoria	1	2	11	15	14	11	6							60	30.60

	Second arch gill rakers														
	21	22	23	24	25	26	27	28	29	30	31	32	33	*N*	$\bar{x}$
Hy. australis															
New South Wales			1	--	7	6	10	16	16	19	17	6	2	100	28.91
Eden, N.S.W.								1	--	--	--	1		2	30
Hybrid-Eden								1						1	28
Hy. melanochir															
Eden		1												1	22
Victoria	1	5	10	17	20	4	2							59	24.19

	Total vertebrae								
	55	56	57	58	59	60	61	*N*	$\bar{x}$
Hy. australis									
New South Wales		7	33	10				50	57.06
Eden, N.S.W.			1	1				2	57.5
Hybrid-Eden					1			1	59
Hy. melanochir									
Eden						1		1	60
Victoria				6	3	2		11	58.64

seum in 1969-70, I visited the Sydney fish market almost every week to obtain fishes. Origin of specimens from throughout New South Wales was determined by identifying the fishery cooperative which offered each box of fish for auction.

On 8 April 1970, I selected, more or less at random, four sea garfishes from several boxes of large specimens from Eden, New South Wales. (These specimens, all females, have been catalogued into the U.S. National Museum collections: USNM 207518-292 mm standard length; 207519-269 mm; 207520-280 mm; and 207521-264 mm). The smallest of the four specimens (USNM 207521) was separated from the other three on the basis of its low gill-raker counts (29 on the first arch, 22 on the second). This count is characteristic of the Victorian population of *Hy. melanochir* (Table 1). Two of the other three specimens (USNM 207518-9) had gill-raker counts typical for *Hy. australis*. The fourth specimen (USNM 207521) had gill-raker counts intermediate between *Hy. melanochir* and *Hy. australis*.

The small specimen of *Hy. melanochir* had 17 dorsal and 19 anal rays in agreement with the modes for the Victorian population (Table 1). The pair of *Hy. australis* had 16 dorsal and 18 anal rays in agreement with the modes for that species. The fourth specimen, like the *Hy. melanochir*, had counts of 17 dorsal and 19 anal rays.

Intermediacy in gill-raker count suggested that the fourth specimen might be a hybrid between *Hy. australis* and *Hy. melanochir;* hence, pigment comparisons were made prior to preservation. There was more yellow on the anterior edge of the anal fin in the small *Hy. melanochir* than in the two *Hy. australis*. The fourth specimen was intermediate. Pigmentation in the pectoral fin was most prominent in the *Hy. melanochir* and the fourth specimen where the melanophores formed a spot distally in the fin. The pigment was distributed all over the fin in the two *Hy. australis*. Scattered small melanophores gave a mottled appearance to the lateral line along the body in the *Hy. melanochir*. This pigment was absent in both *Hy. australis*. A trace of pigment was present in the fourth specimen.

The three larger specimens had a more prominent ridge in the middle of the upper jaw than did the small *Hy. melanochir*. The upper jaw of the *Hy. melanochir* was distinctly shorter than its width (width/length ratio 1.33), in agreement with 35 Victorian specimens of the species (0.92-1.49, mean 1.16). The two *Hy. australis* had the upper jaw about as long as wide (ratios 0.99 and 0.96) as do 32 other *Hy. australis* (0.86-1.29, mean 1.00). The fourth specimen was intermediate (ratio 1.23) between Eden specimens of the two species but within the usual range of *Hy. melanochir* (Figure 1).

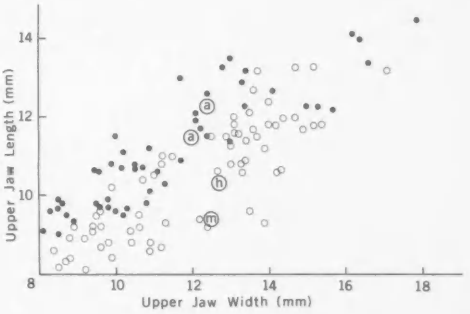

FIGURE 1.—Relationship of upper jaw length to upper jaw width in two species of Australian halfbeaks. Open circles indicate *Hyporhamphus melanochir*; dots *Hy. australis*. Four specimens from Eden, New South Wales indicated by letters: a for *Hy. australis*; m for *Hy. melanochir*; and h for *Hy. australis* × *melanochir*.

Otoliths were extracted from all four specimens while fresh and were examined shortly thereafter by otolith specialist John E. Fitch, who was told only that the four sets of otoliths had come from some Australian halfbeaks. He concluded that two sets (the *Hy. australis*) were of one species, one set (the small *Hy. melanochir*) was of a second species, and the fourth set was intermediate. *Hy. australis* has a much longer (relative to height) sagitta than *Hy. melanochir* (Figure 2). Length divided by height averages (left and right sagittae measured) 1.91 and 1.93 for the two *Hy. australis*, 1.43 for the *Hy. melanochir*, and 1.72 for the fourth specimen. *Hy. australis* has a more pointed rostrum than *Hy. melanochir*, and has a vertical groove near the rostrum on the external side that is

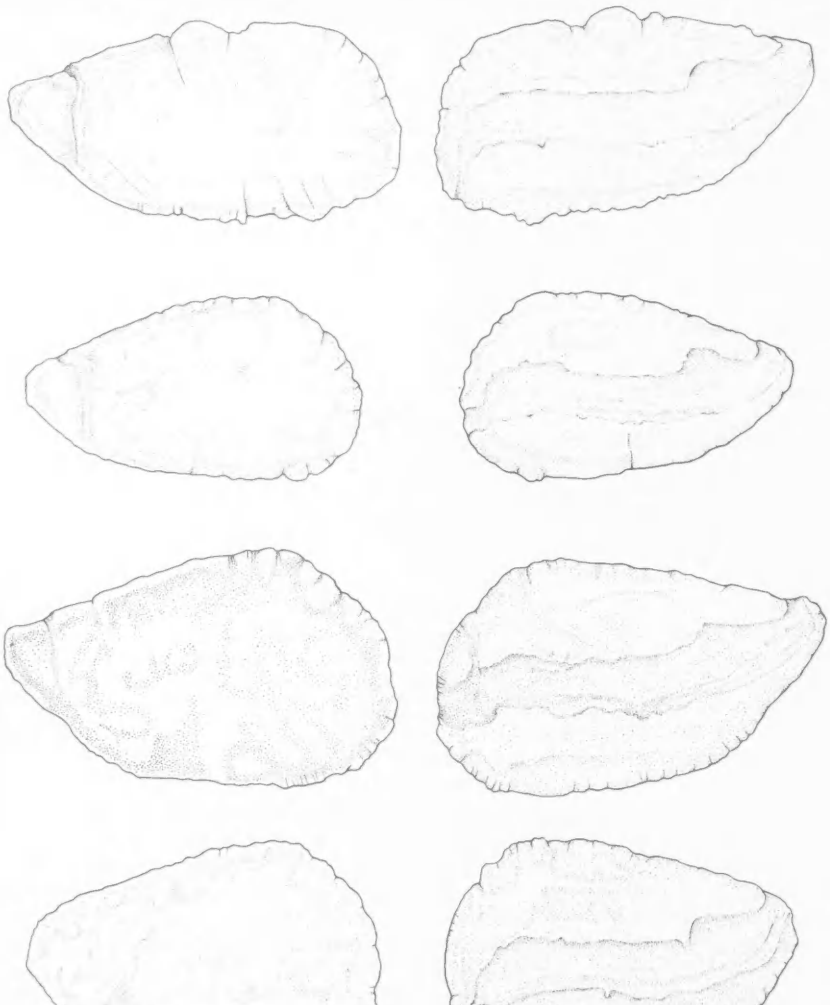

FIGURE 2.—Otoliths (sagittae) of two species of halfbeaks from Eden, New South Wales, Australia. Outer surface on left, inner surface, with sulcus, on right. Top to bottom: *Hyporhamphus australis*, 292 mm SL (standard length); *Hy. australis*, 269 mm SL; *Hy. australis* × *melanochir*, 280 mm SL; and *Hy. melanochir* 264 mm SL.

absent in *Hy. melanochir*. The fourth specimen is intermediate with a faint rostral groove.

Vertebral counts also indicate hybridization. The small *Hy. melanochir* had 60 vertebrae, at the high end of the range for nine Victorian specimens (Table 1). The two *Hy. australis* had 57 and 58 vertebrae, comparing well with 50 New South Wales specimens. The fourth specimen was intermediate with 59 vertebrae.

Based on its intermediacy in gill-raker and vertebral counts, pigmentation, upper jaw length, and otolith structure, I conclude that the fourth specimen is a hybrid between *Hy. australis* and *Hy. melanochir*. The two species are essentially allopatric and show character displacement as their ranges approach, that is, the Victoria population of *Hy. melanochir* differs more from the neighboring New South Wales population of *Hy. australis* than do populations of *Hy. melanochir* from further west, in South Australia and Western Australia (Collette, see footnote 1).

I thank Daniel M. Cohen and Robert H. Gibbs, Jr., for reviewing the manuscript, John E. Fitch for examining the otoliths, Frank J. Schwartz for checking his manuscript on fish hybrids, R. Budd for permitting access to the Sydney fish market, and Keiko Moore for preparing the illustrations.

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CONTRIBUTION ON THE SPAWNING OF *AUXIS* SP. (PISCES, SCOMBRIDAE) IN THE ATLANTIC OCEAN

The frigate mackerel (*Auxis* sp.) are apparently among the most abundant scombrids in the tropical Atlantic Ocean. They form a substantial part of the diet of skipjack tuna, *Katsuwonus pelamis*; yellowfin tuna, *Thunnus albacares* (Dragovich, 1970a); and bluefin tuna, *T. thynnus* (Dragovich, 1970b); and, therefore, it is important to understand their life history and their role in the trophodynamics of tropical ocean ecosystems. We report on the examination of ovaries from 76 frigate mackerel collected from the eastern and western tropical Atlantic, and off Cape Hatteras, N.C. (Figure 1).

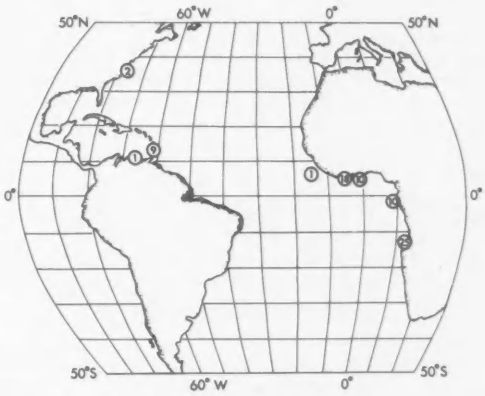

FIGURE 1.—Location and number of *Auxis* sp. captured (in circle) from which ovaries were examined.

The genus *Auxis* may be composed of two species, *A. thazard* (Lacépède) and *A. rochei* (Risso). We were not able to assign the specimens in our study to either species because the published diagnostic characters were not reliable for species identification. More taxonomic work is needed on the genus (William J. Richards, Southeast Fisheries Center, Miami Laboratory,

[1] Contribution No. 222, Southeast Fisheries Center, Miami Laboratory, National Marine Fisheries Service.

National Marine Fisheries Service, pers. comm.).

The ovaries were removed from specimens that had been fixed in 10% Formalin[2] and stored in 40% isopropanol. A wedge-shaped sample was taken from each ovary and about 200 eggs, 0.25 mm (one micrometer unit) in diameter or greater, were measured, following the method described by Clark (1925). The eggs were selected along an edge of the sample corresponding to the radius of the ovary. We determined that eggs below 0.25 mm formed most of the egg-stock present in all mature females throughout the year. In some ovaries, eggs about 0.25 mm in diameter appeared to be in the early stages of yolk accumulation because they were more opaque than the stock eggs. Each ovary was classified according to the following stages:

Stage 1. This stage corresponds to stage 1-S described by Schaefer and Orange (1956): "The gonads are small and ribbon-like. At this stage it is not possible to determine the sex by gross examination. Presumably these are virgin fish that have never yet reached sexual maturity."

Stage 2. The ovaries contained eggs which formed most of the egg-stock. In some ovaries the larger eggs may have been in the early stages of yolk accumulation but did not form a distinct modal group.

Stage 3. The ovaries contained one group of eggs distinctly separated from the egg-stock. Modal diameters of this group were from 0.375 to 0.675 mm.

Stage 4. The ovaries contained two groups of eggs distinctly separated from the egg-stock. Modal diameters of the group formed by the larger eggs were from 0.875 to 0.975 mm.

Selected egg diameter frequency distributions from stages 2, 3, and 4 are shown in Figure 2.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Our evidence indicates that *Auxis* from the tropical Atlantic mature at about 290 mm fork length (Table 1). Fish with ovaries in stages 2, 3, or 4 were considered mature; fish which contained stage 1 ovaries were considered immature. The smallest mature fish (stage 3) from the eastern Atlantic was 270 mm and the largest

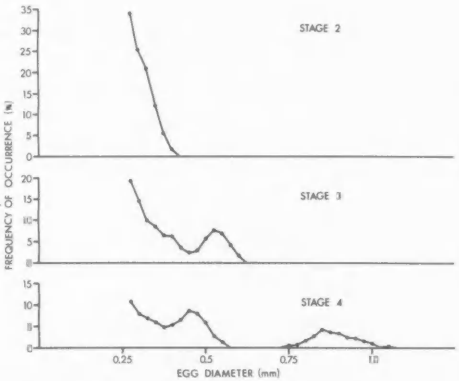

FIGURE 2.—Percent egg diameter frequency distribution from selected ovaries in stages 2, 3, and 4 (smoothed by a moving average of 3).

TABLE 1.—Number of mature and immature *Auxis* examined from the eastern and western tropical Atlantic by 10-mm length intervals.

Length interval (mm)	Eastern Atlantic		Western Atlantic	
	Immature	Mature	Immature	Mature
210-219	1	--	--	--
240-249	2	--	--	--
250-259	1	--	--	--
260-269	2	--	--	--
270-279	1	2	2	--
280-289	1	12	--	--
290-299	--	6	--	--
300-309	--	2	2	1
310-319	--	1	--	2
320-329	--	1	--	--
330-339	--	1	--	--
340-349	--	2	--	2
350-359	--	1	--	--
360-369	--	6	--	--
370-379	--	2	--	--
380-389	--	1	--	--
390-399	--	3	--	--
400-409	--	2	--	--
410-419	--	2	--	--
420-429	--	1	--	1
430-439	--	2	--	--
440-449	--	3	--	--
450-459	--	3	--	--
460-469	--	3	--	--

immature fish was 285 mm. From the western Atlantic, the smallest mature fish (stage 3) was 309 mm and the largest immature fish was 307 mm. There is an indication from the specimens we examined that the eastern Atlantic *Auxis* mature at a slightly smaller size than the western Atlantic *Auxis*. It is possible, however, that this is an artifact resulting from our sample size. Table 1 also indicates the length distribution of specimens used in our study. The two specimens captured off Cape Hatteras were 458 and 459 mm and both had stage 3 ovaries. These are not included in Table 1.

Ovaries in stages 3 and 4 were taken as evidence that spawning was imminent. *Auxis* with ovaries in a spawning condition were captured from the eastern Atlantic in February, March, April, June, September, and October, and from the western Atlantic in March and April. The two specimens from off Cape Hatteras were captured in July and August, and both contained ovaries in spawning condition. The number of *Auxis* examined in each stage of ovary development by month and area of capture is shown in Table 2.

TABLE 2.—Number of *Auxis* examined in each stage of ovary development by month and area of capture.

Area	Stage	Feb.	Mar.	Apr.	June	July	Aug.	Sept.	Oct.
Eastern Atlantic	1	--	--	--	--	--	--	--	8
	2	--	4	2	--	--	--	--	10
	3	1	12	7	2	--	--	10	2
	4	--	--	--	--	--	--	--	6
Western Atlantic	1	--	--	4	--	--	--	--	--
	2	--	--	1	--	--	--	--	--
	3	--	2	3	--	--	--	--	--
Cape Hatteras, N.C.	3	--	--	--	--	1	1	--	--

The number of eggs released per spawning is estimated for five specimens that contained stage 4 ovaries. These were captured off the Ivory Coast on 15 October 1967 at lat 4°31'N, long 5°18'W. The method used to determine the number of eggs released per spawning was to estimate the number in the most mature modal group, assuming that these eggs would be released at next spawning (Simmons, 1969).

The results show that *Auxis* from 360 to 455 mm fork length release from 56,000 to 148,000 eggs (Table 3). Rao (1964) determined

TABLE 3.—Estimated number of eggs in the most advanced mode for *Auxis* of different lengths.

Fork length (mm)	Eggs in the most advanced mode
360	95,000
361	58,000
396	56,000
440	148,000
455	103,000

that a 442-mm frigate mackerel captured off the southwest coast of India would have released 280,000 eggs at next spawning. A large variation should be expected due to the small sample size. The equation describing our regression line calculated by the method of least squares is

$$Y = -127.262 + 0.542X,$$

where Y is the number of eggs in the most advanced mode in thousands and X is the fork length of the fish in millimeters.

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